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By

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A REMARKABLE NEW CRUCIFER FROM MEXICO

REED C. ROLLINS

For over sixty years, the monotypic genus *Ornithocarpa (Cruciferae)* has been known from a single collection made in the state of Jalisco by C. G. Pringle in 1902. That collection was an ample one, and specimens were adequately disseminated so that the uniqueness of *Ornithocarpa fimbriata* Rose has been fully recognized and the authenticity of the species has never been questioned. But the only published information on this unusual species is the rather terse description by Rose (1905) and the somewhat more expanded account in Die Pflanzenfamilien by Schulz (1936). No really new knowledge could be gained without either new collections or from observations on the growing plants in the field.

From time to time, I have encouraged collectors working in Mexico to look for *O. fimbriata* and several attempts have been made to find the plants at the original locality near Constancia Station, east of Guadalajara. The most recent, unsuccessful attempt was that of Dr. Rogers McVaugh of the University of Michigan, who reported that much of the area where the plants might be expected to be found is now under cultivation. Because of the destruction of the original habitat, we had resigned ourselves to the possibility that this highly distinctive and most remarkable genus might never be more adequately known than was possible from the single collection made many years ago.

Fortunately for those of us interested in the *Cruciferae,* a specimen of *Ornithocarpa* showed up in a collection sent for identification by Dr. Peter H. Raven. The specimen, collected by Dr. Dennis E. Breedlove, was in early flower but the unmistakable fimbriate petals and the close match in over-all characteristics to specimens of *O. fimbriata* clearly placed it in the genus *Ornithocarpa.* However, the young ovaries of the flowers had several ovules present instead of two, as in *O. fimbriata,* and the shapes of the very young siliques suggested a fruit quite unlike that of *O. fimbriata* as well. Even with flowering material only, we were nearly certain that an undescribed species was represented by the new collection, which came from the state of Durango. It was added good luck that Dr. Breedlove was returning to Mexico in the summer of 1967, and that he was willing to cooperate to

FIG. 1–3. *Ornithocarpa torulosa*. Breedlove 15888 from Durango, Mex. FIG. 1, greenhouse grown plant showing rhizomes with young plantlets attached. FIG. 2, chromosomes of root-tip cell, no pre-treatment, ×2000. FIG. 3, chromosomes of pre-treated cell, ×2500.

obtain better developed material for study. From Dr. Breedlove's efforts, we now have two additional collections from the Durango locality, one with immature seeds, the other with mature siliques and seeds.

In many respects, *Ornithocarpa torulosa* is a more orthodox crucifer than *O. fimbriata*. At the very least, the silique is like that of many species in other genera of the family, and on that basis alone the presently described species appears to be the more primitive and less specialized of the two species. As in *O. fimbriata*, the siliques of *O. torulosa* are virtually indehiscent. The intact seeds are buoyant in water and readily float. If forcibly submerged and then released, they immediately rise to the water surface. This suggests that seed dispersal is by water transport, at least to some extent. The valves of the siliques are very tightly fused to the replum. When dry, the silique will not dehisce the seeds, even with considerable pressure. However, after 24 hours of soaking in water, the valves do release and the seeds may float away.

We have been successful in germinating the seeds from Breedlove's collection no. 15888 and in growing plants in the greenhouse. The leaves are dark green and quite fleshy. Under conditions of vigorous growth, offset young plants arise from underground rhizomes (Fig. 1) when a plant has reached the 10–15 leaf stage. Proliferation of the plants takes place at a very rapid rate, and in less than two months a six-inch pot is completely filled with the parent plant and its offshoots. Growth is very vigorous, and it is obvious that under natural conditions, the species spreads by these underground rhizomes to form dense patches.

Considerable effort has been expended by Mrs. Lily Rüdenberg[1] in attempts to make satisfactory preparations of the chromosomes of *O. torulosa*. The somatic tissues of the plants have proved to be very difficult to handle, and as yet bud material has not been utilized. The best results were obtained from very young leaves and root-tips. In some figures, there was some uncertainty as to whether one large chromosome or two chromosomes of usual size were present. We have interpreted these as two chromo-

[1] It is a pleasure to thank Mrs. Rüdenberg and to acknowledge her voluntary contribution to our research activity. Also, I want to thank Mrs. Tantravahi for her valuable assistance.

somes, based on our general experience with chromosomes of the *Cruciferae*. A photograph of the chromosomes in a pre-treated root-tip cell is reproduced as Fig. 3.

Mrs. Rüdenberg, after much study, concluded that there were 2n=48 chromosomes in *O. torulosa*. In several figures, we confirmed her interpretations. However, because of the intractability of the material of *O. torulosa,* and a desire to have a wholly new second approach made, we asked Mrs. Ramana Tantravahi to work on the problem. After a number of attempts using several different techniques, she produced excellent preparations from root-tips. A photograph of a root-tip cell without pre-treatment provided by Mrs. Tantravahi is reproduced as Fig. 2. Her preparations confirm the count as 2n=48.

It is clear that *O. torulosa* is a polyploid. However, there is no basis as yet for any suggestion as to the possible origin of the species. It is difficult even to see connections between the genus *Ornithocarpa* and other genera of the family. Schulz (1936) associated it with *Dryopetalon* and *Schizopetalon* in the tribe *Schizopetaleae,* but aside from lobed or more deeply divided petals, these genera have very little else in common. I do not believe they represent a closely interrelated group of genera.

The flower form of *Ornithocarpa* is somewhat like that of *Romanschulzia* and *Thelypodium* in that the parts spread widely from the base and the filaments of all stamens are approximately equal. The white petals of *O. torulosa* spread nearly at right angles to the base of the gynoecium. There is no suggestion of an unguiculate shape to the petals as is so commonly found in the *Cruciferae*. These may be readily seen in Fig. 4.

The greatly elongated inflorescence, the gynophorate silique, and the flower form, including the coiled anthers, all suggest that *Ornithocarpa* is in a general way related to *Romanschulzia* and perhaps to *Thelypodium*. However, I am only willing to support the idea that these genera should be loosely associated together. Certainly, they are not phylogenetically closely related to each other.

Ornithocarpa torulosa Rollins, sp. nov.

Perennial; rhizomatous, stems erect, several to many from an underground rootstalk, simple or branched above, glabrous, somewhat fleshy, 6-10 dm. tall; leaves monomorphic, fleshy, petiolate, pinnate with deeply to shallowly lobed oblong pinnae, glabrous; basal leaves 1-2 dm. long, 2-4 cm. wide,

FIG. 4. Flowers and bud-clusters of *O. torulosa*, ×2. Photo by Frank White.

pinnae up to 2 cm. long, 5 mm. wide, remote; upper cauline leaves reduced and less lobed; inflorescence corymbose, greatly elongating in fruit; lower flowers often bracteate; sepals narrowly oblong to linear, nonsaccate, whitish to light lavender, 5-7 mm. long, ca. 1 mm. wide, one pair with a low horn-like callus at apex of adaxial surface, callus with one to several nearly transparent blunt trichomes; petals white, broadly oblong to obovate in outline, 6-8 mm. long, 2-2.5 mm. wide, upper portion lacerate into slender filaments, margins of lower portion irregularly denticulate; stamens excerted, filaments nearly equal, whitish, 6-8 mm. long, anthers purplish, 2-3 mm. long; four large rounded divaricately ascending glands present on receptacle, each in front of petal insertion, nearly 1 mm. in diameter, persistent; ovary cylindrical, gynophore and style prominent, stigma small, entire; pedicels straight, widely spreading at right angles to rachis or usually slightly ascending, glabrous, expanded at summit, 1-1.5 cm. long; siliques nearly indehiscent, oblong, tapered above and below, flattened parallel to septum, irregularly torulose, 1.5-2 cm. long, 4-5 mm. wide; gynophore 2-3 mm. long, up to 5 mm. long including narrowed portion of lower silique; style 3-5 mm. long; septum complete, translucent; ovules 6-10 in each loculus; seeds wingless and marginless, pearly grey, elliptical to nearly orbicular, somewhat flattened, ca. 4 mm. in diameter, outer seed-coat horny, densely and minutely granulate, inner seed-coat soft and spongy, uneven in thickness; embryo scarcely attached to seed coat, cotyledons accumbent. 2n=48.

Herba perennis glabris; caulibus erectis simplicibus vel superne ramosis 6-10 dm. altis; foliis pinnatis petiolatis inferne 1-2 dm. longis, 2-4 mm. latis; inflorescentiis corymbosis; floriis inferne bracteatis superne ebracteatis; sepalis nonsaccatis 5-7 mm. longis, ca. 1 mm. latis; petalis albis ablongis vel abovatis superne laciniatis 6-8 mm. longis, 2-2.5 mm. latis; pedicellis rectis patentibus 1-1.5 cm. longis; siliquis stipitatis oblongis compressis 1.5-2 cm. longis, 4-5 mm. latis; stylis 3-5 mm. longis; stigmatis minutis integris; seminibus griseis immarginatis ellipticis vel orbicularibus compressis; cotyledonibus accumbentibus.

Holotype in the Gray Herbarium collected from a moist field 2 miles west of Coyotes along Mexican Highway 40, 5 miles east of El Salto, Durango, Mexico, 25 July 1967, *D. E. Breedlove 15757*. (Isotype DH; others to be distributed.) Other specimens studied, from the same locality, 16 June 1966, *D. E. Breedlove 14331* (GH); 13 August 1967, *D. E. Breedlove 15888* (GH).

Literature Cited

Rose, J. N. 1905. Studies of Mexican and Central American Plants—No. 4. Contrib. U. S. Nat. Herb. 8:293.

Schulz, O. E. 1936. Cruciferae. Die Natüralichen Pflanzenfamilien **17b**:402–405.

PETAL COLOR POLYMORPHISM IN LEAVENWORTHIA (CRUCIFERAE)

David G. Lloyd[1]

Balanced polymorphism provides some of the most striking examples of variation in natural populations and the study of it has contributed to an understanding of many aspects of population biology (Ford, 1964). In plants, polymorphism associated with chromosome structure and breeding systems (self-incompatibility, dioecy, etc.) has been extensively studied. In addition, polymorphic variation has been demonstrated in a wide range of plant characters including seeds, fruits, chemical compounds produced, and vegetative morphological characters (Huxley, 1955; Heslop-Harrison, 1964; Jones, 1967). Some of these studies, particularly those of New (1958) on seeds of *Spergula arvensis* and of Daday (e.g., 1965) and Jones (1966) on the cyanogenesis pathway in legumes, have provided considerable information on the selective forces determining genotypic frequencies.

Polymorphic variation in petal color has been reported in a considerable number of Angiosperms, but has rarely been studied intensively. Hovanitz (1953) demonstrated a correlation between petal color frequencies and sun exposure in *Hepatica triloba.* Epling *et al.* (1960) showed that petal color frequencies in *Linanthus parryae* were remarkably stable and described clines, probably due to recent hybridization. Joshi and Jain (1964) described clinal variation in flower color frequency in *Justicia simplex.*

The present paper describes the petal colors found in *Leavenworthia* and their distribution and frequency in natural populations. The genetics of some of the morphs is described, and some of the factors determining the frequency of morphs are investigated.

Species and Races of Leavenworthia

The following description of the species of *Leavenworthia* is based on the accounts of Rollins (1963) and Lloyd (1965). *Leavenworthia* is a small, distinct genus of the *Cruciferae,* con-

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taining seven species restricted to the south central United States. The species are separated by strong isolating barriers, with the exception of *L. crassa* Rollins and *L. alabamica* Rollins, which readily hybridize under experimental conditions and in cultivated fields where they have come into contact. Three chromosome numbers (n=11, 15 and 24) are found in the genus and divide the species into three natural groups (Table 1).

Most of the species contain two or more geographic races. The allopatric races within each species are distinguished by consistent, although sometimes minor, morphological features (other than flower color) and in all combinations tested produce vigorous and fertile inter-racial hybrids. A total of 29 distinguishable races, some of which have been named as varieties by Rollins (1963), have been recognized to date in the seven species (Tables 1 and 2). The most complex species so far investigated is *L. crassa*, with 15 allopatric races in northwest Alabama, the most distantly separated of which are only 11 aerial miles apart. *Leavenworthia alabamica* has six known geographic races, occurring over a larger area in northwest Alabama. The other species have been studied less intensively, but appear to be less complex and have fewer, well-separated and more widespread races.

TABLE 1. The species of *Leavenworthia*

Species	*Chromosome number* (n)	*No. known geographic races*	*Breeding system of races*[1]
L. crassa	11	15	4 si, 11 sc
L. alabamica	11	6	1 si, 5 sc
L. exigua	11	3	sc
L. aurea	24	1	sc
L. stylosa	15	2	si
L. torulosa	15	1	sc
L. uniflora	15	1	sc

[1]si = self-incompatible (with considerable pseudo-compatibility), sc = self-compatible.

The plants are winter-annuals, which before the advent of agriculture were restricted to small isolated clearings (cedar glades) in the forest on limestone and dolomitic limestone outcrops. In the Central Basin of Tennessee, glade populations may be scattered more or less continuously over an acre or more. Elsewhere, glade populations are usually small and discrete, with well-defined limits determined by soil conditions, and often contain less than a thousand plants. Following the removal of forest around the

glades in some areas, *Leavenworthia* plants have moved onto a variety of secondary sites, most commonly pastures, corn fields and wasteland. The secondary populations sometimes occupy several acres and contain more than a hundred thousand plants. In this study, a population is defined as a more or less continuous series of plants, separated from other plants by a clear distribution gap or a physical barrier to easy dispersal.

Petal Colors Occurring in Nature

Variation in flower color is determined by the nature and distribution of the pigment in the petals. The pigment is either yellow, cream or orange. The three colors can be distinguished easily and with complete accuracy. The nature of the pigments, which are carried in chromatophores, is not known. The pigment in the petals is distributed in one of four patterns (Fig. 1): (a) *uniform*—the pigment is uniformly distributed over the petal limb; (b) *centered*—the proximal portion of the petal limb is pigmented and abruptly delimited from the unpigmented, white distal portion; (c) *eye-intermediate*—the proximal portion of the petal is pigmented, and grades into the distal portion, which is white or almost white; (d) *strip-intermediate*—proximal and distal pigmented areas are separated by a white strip of varying width. The centered and uniform patterns show little variation within populations. The extent of pigmentation in flowers with intermediate patterns, however, varies considerably between individuals of the same population. The two intermediate patterns can usually be distinguished from each other and from the centered and uniform patterns, but in populations containing plants with intermediate pigment patterns occasional plants are difficult to classify.

The flowers of one plant all have the same pigment color and distribution. If more than one pattern and pigment occur in a population, the patterns occur in similar proportions in flowers with different pigments; color and pigment distribution vary independently. Yellow is by far the most common petal color in the *Leavenworthia* populations studied. Plants with orange-pigmented or cream-pigmented flowers are rare or absent in most populations. Plants with either of the two intermediate patterns are also absent or rare in natural populations. Consequently, the two intermediate patterns have not been found in cream- and

FIG. 1. The four pigment patterns found in flowers of natural *Leavenworthia* populations. Top left: centered. Top right: uniform. Bottom left: strip-intermediate. Bottom right: eye-intermediate.

orange-pigmented flowers. The flowers of natural populations can thus be classified into the following six colors (morphs).

1. Yellow-centered: the only color in many populations and common in many polymorphic populations.
2. Yellow (uniform yellow): the only color in many populations and common in many polymorphic populations.
3. Eye-intermediate: rare or absent and found only in yellow-pigmented flowers.
4. Strip-intermediate: rare or absent and found only in yellow-pigmented flowers.
5. Orange-pigmented: usually rare or absent, occasionally common, and distributed only in the uniform and centered patterns.
6. Cream-pigmented: rare or absent, and distributed only in the centered and uniform patterns.

The appearance of the morphs varies somewhat between races. For example, the pigmented center of yellow-centered flowers is of different lengths in different races. The yellow pigment may not be identical in all species; in *L. aurea* it imparts an orange-yellow color to the petals, but in other species it is light yellow. The orange-brown nectar guides (Fig. 1) are present in all flowers and vary little in any race.

Distribution and Frequency of Morphs

Natural populations of all except three of the 29 races (*L. exigua* var. *laciniata, L. exigua* var. *lutea* and *L. aurea*) were examined in the 1961, 1962 or 1964 flowering seasons. The flower colors present and their frequencies were recorded for a number of populations of each race, except for those races of *L. crassa* and *L. alabamica* which exist as only one or two populations (Table 2). In populations with less than one thousand plants, the number of plants with each flower color was counted. In larger populations, the flower color of at least five hundred plants in a transect across the population was recorded. Observations on the races of the four uniformly self-compatible species have been combined with data from Rollins (1963) in Table 2.

On the basis of the number and frequency of the flower colors present, the *Leavenworthia* populations fall into three classes. In addition, within the limits noted below, the populations of a race are similar in the morphs present and their relative frequencies. Consequently, the races themselves may be grouped into three classes. The three types of races are not absolutely distinct,

TABLE 2. The breeding system and flower colors of the geographical races of *Leavenworthia* species

Species	*Race or variety*	*Breeding system*[1]	*No. populations examined*[2]	*No. colors found*	*Flower Color Description*[3]
stylosa	white-flowered	si	12	4	QM–yellow-centered
"	yellow-flowered	si	14	5	QM–yellow
torulosa	–	sc	>100	2*	MM–yellow-centered
uniflora	–	sc	>100	1	MM–yellow-centered
crassa	c1	si	8	6	QM–yellow-centered
"	c2	si	11	5	QM–yellow-centered
"	c3	si	8	6	PM–yellow-centered + yellow
"	c4	si	4	5	QM–yellow-centered
"	c5	sc	9	4	PM–yellow-centered + yellow
"	c6	sc	1	1	MM–yellow-centered
"	c7	sc	2	3	PM–yellow-centered + yellow
"	c8	sc	1	3	PM–yellow-centered + yellow
"	c9	sc	1	1	MM–yellow-centered
"	c10	sc	1	2	PM–yellow-centered + yellow
"	c11	sc	1	1	MM–yellow-centered
"	c12	sc	1	1	MM–yellow
"	c13	sc	2	1	MM–yellow
"	c14	sc	1	1	MM–yellow-centered
"	c15	sc	13	1	MM–yellow
alabamica	a1	si	17	3	QM–yellow-centered
"	a2	sc	14	3*	MM–yellow-centered
"	a3	sc	1	1	MM–yellow-centered
"	a4	sc	11	1	MM–yellow-centered
"	Russellville	sc	1	2	PM–yellow-centered + orange-centered
"	Tuscumbia	sc	3	1	MM–yellow-centered
exigua	var. *laciniata*	sc	1	1	MM–yellow-centered
"	var. *exigua*	sc	>50	1	MM–yellow-centered
"	var. *lutea*	sc	5	1	MM–yellow
aurea	–	sc	10	1	MM–yellow

[1] si = self-incompatible, sc = self-compatible.
[2] For those races of which only one or two populations were examined, these are the only known populations.
[3] QM = quasimorphic, PM = polymorphic, MM = monomorphic.
* All except one or two populations were strictly monomorphic—see text.

but represent readily distinguishable ranges of flower color frequencies.

MONOMORPHIC RACES: Seventeen races, distributed among all species except *L. stylosa*, are completely uniform, or almost so, in flower color (Table 2). Twelve races have yellow-centered flowers and five races have yellow flowers. More than three hundred populations of monomorphic races have been examined and only three contained any variation in flower color. In one population of *L. torulosa*, Rollins (1963) observed a few yellow-flowered plants among the plants with yellow-centered flowers. One of the fourteen counted populations of race *a2* of *L. alabamica* contained a single plant with eye-intermediate flowers among the yellow-centered plants and another contained two plants with cream-pigmented flowers.

QUASIMORPHIC RACES: Six races of *L. stylosa*, *L. crassa* and *L. alabamica* contain some populations which are strictly monomorphic while others have the same morph in high frequency, but also include plants of one or more additional morphs in low frequencies. These races are described here as quasimorphic. The predominant flower color in five of these races is yellow-centered, but in the yellow-flowered race of *L. stylosa* the predominant color is yellow (Tables 2 and 3). Altogether, 44 of the 66 populations of quasimorphic races examined contained more than one morph. In 41 of these, one color occurred in frequencies between 98 and 100 per cent. The predominant color occurred in less than 98 per cent of the plants in only three populations, which contained up to 24.6 per cent of the otherwise rare orange-pigmented morph.

Thus, populations of the quasimorphic races characteristically contain two or more morphs, but only one of these is common. The occurrence of strictly monomorphic populations in these races shows that the quasimorphic races are not sharply distinct from the monomorphic races. Conversely, the three populations of the quasimorphic races *c2* and *c4* of *L. crassa* in which orange-pigmented flowers are relatively common may be described as polymorphic. But, in contrast to the polymorphic races, the presence of two morphs in intermediate frequencies is not characteristic of races *c2* and *c4*.

In addition to the common morph, populations of the quasimorphic races contain up to four rare flower colors. Most of the

six morphs have been found in one or more populations of all six quasimorphic races (Table 3), but different populations of one race contain different rare morphs. Almost every possible combination of the presence and absence of the rare colors occurs in the quasimorphic races, and their relative frequencies vary irregularly. A rare morph may arise periodically as a mutant, and persist for an indefinite time, depending on chance and the balance of selective forces operating on it.

POLYMORPHIC RACES: All populations of six races contained two morphs in frequencies of at least three per cent, and usually more than 20 per cent. In five of these polymorphic races (*c3*, *c5*, *c7*, *c8* and *c10* of *L. crassa*) the yellow and yellow-centered morphs were common (Tables 2 and 3). Some of the polymorphic *L. crassa* populations also contained one or more rare morphs in low frequencies. In the only known population of the Russellville race of *L. alabamica*, the yellow-centered and orange-centered morphs are common (Table 3).

Except for races *c3* and *c5* of *L. crassa*, the polymorphic races are known from only one or a few populations. The frequencies of the morphs in races *c3* and *c5* were counted in populations occupying glade, pasture, roadside and corn-field sites. Many more populations of these races were observed than were actually counted. All of these consisting of more than a few dozen plants contained the yellow and yellow-centered morphs in considerable frequencies. The polymorphism in these races, therefore, persists in a wide variety of habitats. In many populations of the polymorphic races, the morph frequencies were similar in 1961, 1962 and 1964. In the only polymorphic population in which exactly the same area was counted in two years, the ratios of yellow-centered to yellow to eye-intermediate morphs were determined from approximately one thousand plants, and were similar in both years (68.3:28.3:3.31 in 1961; 70.0:26.8:3.25 in 1962).

The glade populations of the polymorphic races never occupy an area more than about 30 meters long, and the frequency of the morphs varies little throughout a glade. On secondary sites, populations which are more or less continuous for several acres contain the yellow and yellow-centered morphs throughout, but their relative frequency is locally variable. Such populations may change from predominantly yellow to predominantly yellow-centered over a distance of 20 meters or less. Two populations of

TABLE 3. The ranges of morph frequencies in populations of quasimorphic and polymorphic races

	Species	Race	No. populations counted	Range of morph frequency (percentage)					
				Yellow-centered	Yellow	Eye-intermediate	Strip-intermediate	Orange-pigmented	Cream-pigmented
Quasimorphic races	*stylosa*	white-flowered	12	99.0-100	0-0.9	0-0.3	0-0.5	0[1]	0
	stylosa	yellow-flowered	14	0-0.7	99.0-100	0-0.7	0-0.5	0	0-0.5
	crassa	c1	8	98.9-100	0-0.9	0-0.1	0-0.1	0-0.1	+
	crassa	c2	11	94.3-100	0-0.6	0-0.5	0-0.5	0-5.1	+
	crassa	c4	4	75.4-99.8	0-0.1	0-0.7	0	0-24.6	+
	alabamica	a1	17	98.2-100	0-1.6	0-0.2	0	0	0
Polymorphic races	*crassa*	c3	8	41.8-91.3	7.9-58.2	0-3.3	+	+	+
	crassa	c5	9	3.0-94.5	4.6-97.0	0-0.9	0	0	+
	crassa	c7	2	78.2-94.3	20.7-5.0	1.1-0.7	0	0	0
	crassa	c8	1	52.2	47.6	0.3	0	0	0
	crassa	c10	1	69.1	30.9	0	0	0	0
	alabamica	Russellville	1	86.4	0	0	0	13.6	0

[1] A zero indicates a morph has not been found in a race; a plus sign indicates a morph did not exceed 0.05 per cent in any of the populations counted.

race *c5* on uncultivated land in 1962 were divided into numerous, more or less discrete, sub-populations of varying size. The frequency of the morphs in these sub-populations varied from all yellow to all yellow-centered in an irregular pattern. Both of these populations were on formerly cultivated land and were probably continuous in previous years. Reduction of these populations to small scattered patches of plants may have resulted in genetic drift of allele frequencies and to loss of one allele in some sub-populations.

Thus, within the limits described, pure populations of each of the 29 *Leavenworthia* races exhibit a restricted range of flower color frequencies. Six types of races can be distinguished (Table 2):

1. Monomorphic yellow (five races).
2. Monomorphic yellow-centered (twelve races).
3. Quasimorphic yellow (one race).
4. Quasimorphic yellow-centered (five races).
5. Polymorphic yellow plus yellow-centered (five races).
6. Polymorphic yellow-centered plus orange-centered (one race).

There is some overlap in morph frequencies between populations of different race types, but the six race types each have a characteristic, limited spectrum of morph frequencies.

Secondary Polymorphism

Polymorphic populations of a different kind from those described above have recently arisen in *L. crassa* and *L. stylosa,* following the removal of forest and spread of populations from the original glade sites onto cultivated and waste land. The 'white-flowered' and 'yellow-flowered' races of *L. stylosa* were completely, or almost completely, allopatric before the removal of forest, but glade populations of the two races approach each other over a broad front in the Central Basin of Tennessee (Rollins, 1963). Since the advent of agriculture, the two races have formed polymorphic populations in three areas in Wilson Co., Tenn. Although the micro-distribution of the two morphs in the hybrid areas is complex, there are a number of short clines where populations change from about 98 per cent yellow-centered to about 98 per cent yellow-flowered plants within a few hundred meters. In Morgan Co., Alabama, eleven races of *L. crassa* and two races of *L. alabamica,* each originally confined to one or a

few cedar glades, occur within an area of approximately ten square miles (Lloyd, 1965). Many of these races have now spread onto cultivated land, and on at least ten occasions have formed mixed, polymorphic populations. In both species, the secondary polymorphic populations contain the yellow and yellow-centered morphs. But, in contrast to the racially pure populations, the mixed populations show a complete gradation from yellow to yellow-centered populations, with all frequencies of the two morphs represented.

Distribution of the Race Types

The six racial types distinguished on the basis of petal color frequencies are not randomly distributed among the *Leavenworthia* species or among the races in the complex species *L. crassa* and *L. alabamica* (Table 2). The most important factor influencing the petal color diversity of the races is the breeding system. The primitive breeding system in *Leavenworthia* is self-incompatibility with some pseudo-compatibility, as found at present in seven races of *L. stylosa, L. crassa* and *L. alabamica* [Tables 1 and 2, from data in Rollins (1963) and Lloyd (1965)]. The remaining 22 races are self-compatible, giving equally frequent fruit set on self- and cross-pollination. Self-compatibility has evolved at least six times in the genus and has been accompanied by evolutionary trends in more than fifteen characters. The extent of evolution in these characters varies considerably in self-compatible races. In *L. crassa* and *L. alabamica*, the amount of spontaneous autogamous pollination in an insect-free greenhouse is least in the self-incompatible races and highest in races which show the greatest number of characters associated with self-compatibility (Lloyd, 1965). In general, the percentage of self-fertilization in natural populations of the races probably increases with increasing expression of characters associated with self-compatibility.

There is a marked tendency for the number of flower color morphs found in a race to decrease as the adaptations to self-pollination and, presumably, the amount of inbreeding increase (Table 2). This trend is evident in the whole genus, but is more regular when the species or species groups are considered separately. In the species with 15 chromosome pairs, the two races of

L. stylosa, which are self-incompatible, have up to four and five flower colors per population respectively. The self-compatible species *L. torulosa* has two morphs, one of which was present in only one population. The species with flowers best adapted to autogamy, *L. uniflora*, has only plants with yellow-centered flowers.

In *L. alabamica* (n=11), the only self-incompatible race, *a1*, has up to three morphs in each population. Race *a2* is self-compatible, but does not show any of the floral features usually associated with self-compatibility (Lloyd, 1965). Most populations of race *a2* are strictly monomorphic, as described above. The remaining self-compatible races have reduced flowers and other adaptations to self-pollination and are monomorphic, except for the one known population of the Russellville race.

The four self-incompatible races in *L. crassa* (n=11), each have five or six petal color morphs. Race *c5*, which shows the least adaptation to autogamy among the self-compatible races, has four morphs. Races *c6* to *c10*, which show an intermediate loss of adaptations to cross-pollination and a gain of characters facilitating self-pollination, have between one and three morphs. Races *c11* to *c15* are best adapted to self-pollination and are also strictly monomorphic.

The four races of *L. exigua* (n=11) and *L. aurea* (n=24), which have lost more of the adaptations to cross-pollination than any of the races of *L. crassa* or *L. alabamica*, are all strictly monomorphic.

In several phyletic lines, therefore, the number of morphs found in a race decreases as the facility for autogamous pollination increases. But it is noteworthy that all except one of the six polymorphic races, the populations of which contain two *common* morphs, are self-compatible. Moreover, all of the glade populations of the polymorphic races are small, usually containing less than two thousand plants. The polymorphic races therefore often exist in their natural habitat in small, inbred populations. The most extreme case of the maintenance of a polymorphism under such adverse conditions is the single existing population of race *c10* of *L. crassa*. This population is not only self-compatible, but has introrse anthers and automatically self-pollinates itself with considerable frequency in an insect-free greenhouse (Lloyd, 1965). In 1962 the polymorphic population consisted of 127 flow-

ering plants, which produced an estimated average of 1.68 flowers per plant. In 1964, the population contained about 60 small plants at the beginning of the flowering period.

The yellow-centered plus orange-centered polymorphism is restricted to the Russellville race of *L. alabamica,* which is known from, and may well exist as, a single population. The other five polymorphic races, which have the yellow and yellow-centered morphs in all populations, are races of *L. crassa* and occur within a single area approximately three miles long by one mile wide in Morgan Co., Alabama (Lloyd, 1965). These races are distinguishable by minor, but consistent, morphological characters and each occupies one or a few cedar glades from which they have spread onto cultivated land. The polymorphism has the same genetic basis in at least three of the races (see below) and is restricted to this area. It is therefore probable that the yellow plus yellow-centered polymorphism in *L. crassa* has evolved only once and has been retained in the differentiation of the five polymorphic races. Six other races of *L. crassa* occur in the same small area. They are either monomorphic yellow or monomorphic yellow-centered and are, in general, more adapted to inbreeding than the polymorphic races. These monomorphic races have probably been derived from polymorphic ancestors by loss of one of the alleles.

Genetics

Plants of several races of *L. crassa,* race *a1* of *L. alabamica* and both races of *L. stylosa,* were grown in a greenhouse from seed collected from natural populations. In addition, the natural progeny of several plants of the rare morphs of races *c1, c2* and *c3* of *L. crassa* and race *a1* of *L. alabamica* were grown. A number of crosses were made, and the F_1 plants grown. Many plants died and only small numbers from some of the families flowered. Very few families were taken to the second generation.

Crosses within populations.

Yellow-centered versus yellow: In the quasimorphic yellow-centered races *c1* and *c2* of *L. crassa,* the natural progeny of yellow-centered plants were all yellow-centered. The natural progeny of four yellow-flowered plants were a mixture of plants with

yellow flowers and plants with yellow-centered flowers, in approximately equal numbers. F_1 and F_2 families from yellow-centered × yellow-centered crosses in race *c2* consisted entirely of plants with yellow-centered flowers (Table 4). The families from yellow × yellow and yellow × yellow-centered crosses segregated for yellow and yellow-centered morphs. These results suggest that the difference between yellow and yellow-centered is determined at a single locus, that yellow is dominant to yellow-centered, and that the rare yellow-flowered plants are heterozygous.

In the polymorphic races *c3*, *c5* and *c8* of *L. crassa*, yellow-centered × yellow-centered and yellow-centered × yellow crosses produced F_1 and F_2 families in which the plants were either all yellow-centered or segregated for both morphs (Table 4). Yellow × yellow crosses produced only yellow-flowered plants. The results indicate that the alleles of one locus determine the difference between the two flower colors, that the three genotypes occur in nature, and that yellow-centered is dominant to yellow.

Although the genetic analysis of yellow-centered versus yellow flowers in these races is incomplete, it is clear that the genetic basis of the two color patterns is different in the quasimorphic and polymorphic races. Also, it may be noted that neither of the intermediate pigment patterns appeared in any cross, so these patterns are not produced by heterozygotes for alleles determining the uniform and centered patterns.

Intermediate patterns: The natural seed of four strip-intermediate and two eye-intermediate plants of the quasimorphic yellow-centered races of *L. crassa* and *L. alabamica* were collected. The progeny were grown and in each case contained approximately equal numbers of yellow-centered plants and intermediate plants of the same type as the seed parent. A strip-intermediate × yellow-centered cross in race *c2* produced four yellow-centered and four strip-intermediate plants. This information suggests that the intermediate patterns, like yellow, may be dominant to yellow-centered in the quasimorphic races. It is not known whether the two intermediate patterns are determined by alleles of the same locus or if homologous loci are involved in all quasimorphic races of *L. crassa* and *L. alabamica*.

The natural progeny of three eye-intermediate plants of the polymorphic races *c3* and *c5* of *L. crassa* and the F_1 progeny of a yellow-centered × eye-intermediate cross (race *c3*) were in each

TABLE 4. The genetics of yellow-centered versus yellow flowers in four races of *L. crassa*.

Race	*Parents*		*First generation*		*Second generation*		
	Cross	*Description*	*Number y.c.*	*Number yellow*	*Cross*	*Number y.c.*	*Number yellow*
c2	623-1 × 621-8	yellow × y.c.	16	14	y.c. × y.c.	5	0
					yellow × yellow	4	8
					y.c. × yellow	12	9
	621-8 × 621-9	y.c. × y.c.	17	0			
	621-17 × 621-16	y.c. × y.c.	16	0			
	623-1 × 623-1	yellow selfed	3	1			
	1290 × 1291	y.c. × yellow	13	13			
c3	121-7 × 121-12	y.c. × yellow	23	0	y.c. × y.c.	11	2
					y.c. × yellow	7	4
	121-7 × 121-7	y.c. selfed	8	0			
	121-12 × 121-12	yellow selfed	0	9			
	635-14 × 635-9	y.c. × yellow	14	12	y.c. × y.c.	19	4
					yellow × yellow	0	9
	635-13 × 635-14	y.c. × y.c.	20	0			
	635-9 × 606-15	yellow × yellow	0	32			
	605-6 × 602-2	yellow × yellow	0	19			
	635-17 × 635-19	y.c. × y.c.	5	4			
c5	632-6 × 632-1	y.c. × yellow	5	3			
	632-8 × 632-6	y.c. × y.c.	9	3			
	632-6 × 632-6	y.c. selfed	3	0			
	632-1 × 632-1	yellow selfed	0	13			
c8	631-12 × 631-21	y.c. × yellow	10	6			
	631-21 × 631-21	y.c. selfed	1	2			

case a mixture of the yellow, yellow-centered and eye-intermediate morphs. The eye-intermediate phenotype may be controlled by a dominant gene at a separate locus from, and epistatic to, the alleles controlling the yellow plus yellow-centered polymorphism.

CROSSES BETWEEN RACES.

A number of crosses between plants of different races were made, using only plants with yellow or yellow-centered flowers. Flowering F_1 plants were obtained in 13 families from crosses between *L. crassa* races and three families from crosses between the two *L. stylosa* races. The outstanding feature of the crosses between races is that, in most families, some or all of the hybrids had flowers with neither the centered nor the uniform pigment patterns of the parents, but with an intermediate pattern; that is, dominance was often incomplete. In both species, there was a marked tendency for the intermediate flowers to resemble the dominant pigment pattern least in families in which the proportion of plants with intermediate pigment patterns was highest. In

TABLE 5. Petal and pistil measurements of yellow-centered and yellow flowers of seven *L. crassa* races[1]

Race	Population	Av. pistil length mm (1)	Av. notch length mm (2)	Av. petal length mm (3)	Pistil : Petal (1)÷(3)	Notch : Petal (2)÷(3)	Difference between morphs[2] Pistil : Petal	Difference between morphs[2] Notch : Petal
c1	171	5.34	1.32	12.20	.438	.1083	−.014	−.006
		5.35	1.35	11.83	.452	.1139		
	954	5.48	1.03	11.89	.461	.0868	−.058	+.016
		5.54	0.75	10.67	.519	.0707		
c2	354[3]	5.45	0.95	12.13	.449	.0789	−.009	−.006
		5.25	0.97	11.46	.458	.0849		
	354	4.81	1.05	11.60	.414	.0902	−.031	+.011
		4.88	0.87	10.98	.445	.0794		
	368	4.61	1.16	11.07	.417	.1050	−.046	+.013
		4.66	0.93	10.06	.463	.0923		
c3	89[3]	5.97	1.39	12.46	.480	.1122	−.064	+.021
		6.34	1.06	11.66	.544	.0909		
	89	5.65	1.33	11.13	.507	.1195	−.062	+.027
		5.67	0.92	9.95	.569	.0924		
	61	6.46	1.26	12.47	.518	.1014	−.080	+.009
		6.82	1.06	11.41	.598	.0925		
	792	6.52	0.97	11.80	.553	.0828	−.091	+.010
		7.03	0.80	10.93	.644	.0732		
c5	100	6.18	1.47	12.43	.497	.1184	−.063	+.016
		6.25	1.14	11.16	.560	.1025		
	58	6.26	1.45	12.71	.492	.1143	−.074	+.024
		6.32	1.00	11.17	.566	.0899		
	96	6.18	1.17	11.49	.538	.1021	−.058	+.002
		6.67	1.11	11.18	.596	.0997		
	86	5.91	1.12	11.15	.530	.1005	−.074	+.009
		6.04	0.92	10.00	.604	.0912		
c7	361	3.92	0.84	9.28	.422	.0899	−.044	+.025
		3.95	0.55	8.48	.466	.0648		
	927	4.18	0.83	10.03	.417	.0824	−.052	+.014
		4.26	0.62	9.09	.469	.0684		
c8	72[3]	5.16	0.76	9.45	.546	.0804	−.088	+.030
		5.45	0.44	8.61	.634	.0508		
	72	5.16	0.93	10.04	.514	.0929	−.077	+.026
		5.31	0.60	8.98	.591	.0672		
c10	698	5.03	0.88	10.03	.501	.0884	−.065	+.012
		5.04	0.68	8.93	.566	.0760		

[1] The measurements and ratios for yellow-centered flowers of each sample are shown above the corresponding figures for yellow flowers.

[2] Ratio for yellow-centered flowers minus ratio for yellow flowers.

[3] Populations 354, 89 and 72 were sampled in 1962 and 1964.

the *L. crassa* crosses, the intermediate flowers resembled the naturally occurring eye-intermediate pattern, but in *L. stylosa* the intermediate flowers resembled the strip-intermediate pattern.

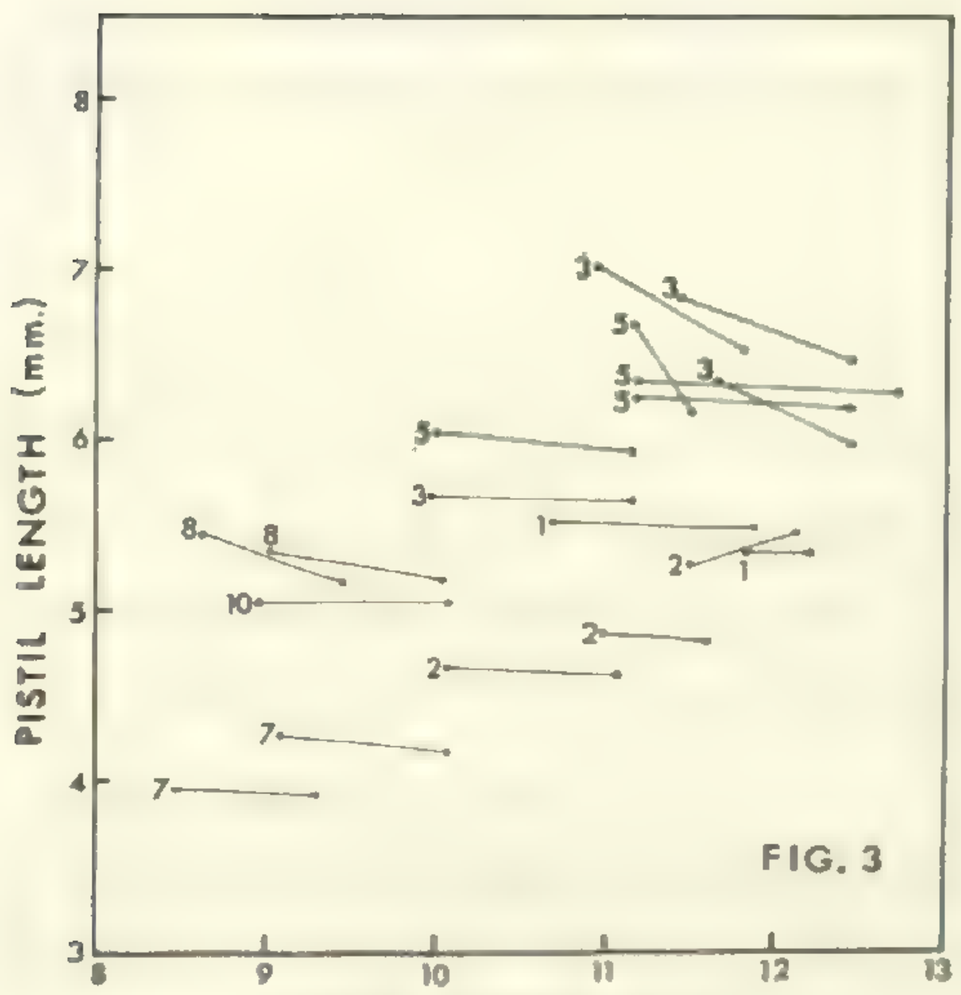
The greatest variability in the pigment pattern of hybrids between races was noted when a heterozygous yellow-centered plant of the polymorphic race *c*3 of *L. crassa* was crossed with a heterozygous yellow plant of the quasimorphic race *c*2. The F_1 family of 15 plants consisted of four plants with yellow-centered flowers, one yellow-flowered plant, six plants with eye-intermediate flowers (the extent of pigmentation varied between plants) and four plants with variable flower colors. The variable plants produced yellow-centered, yellow and a full range of intermediate flowers throughout their flowering period, and in some flowers the extent of pigmentation varied among the four petals (Fig. 2). Scapose flowers were mostly yellow-centered or nearly so. Most racemose flowers were uniformly or almost uniformly yellow.

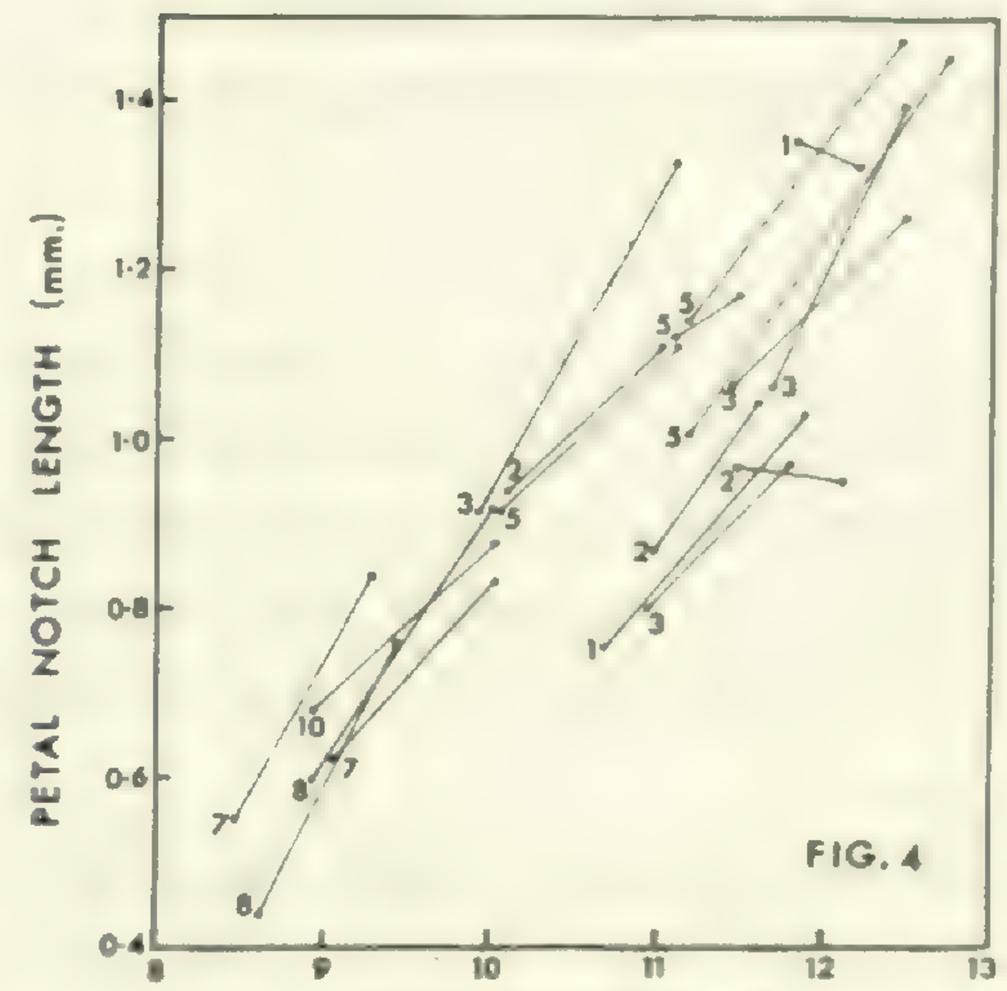
Flower Measurements

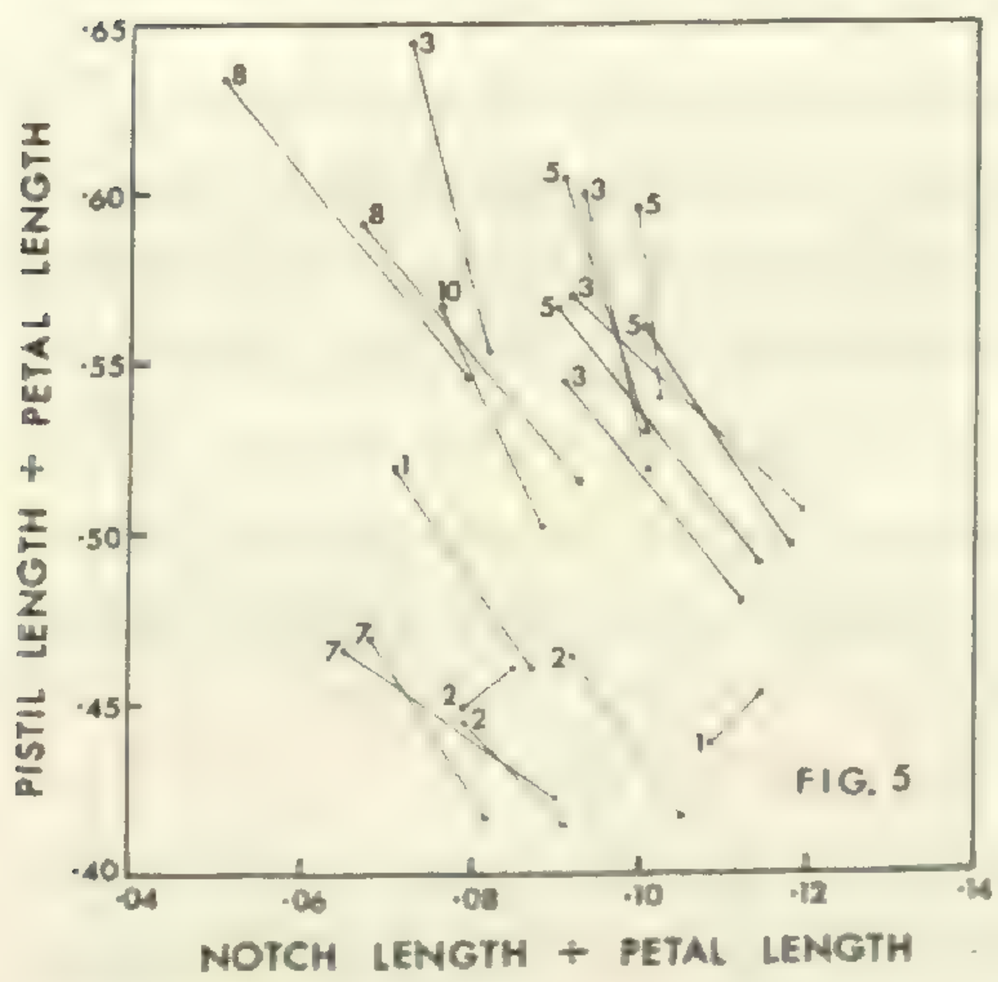
Yellow-centered and yellow flowers of seven races of *Leavenworthia crassa* were compared to determine whether there were any differences between the flowers in addition to the pigment patterns. Eighteen samples from 15 natural populations (Table 5) were collected by taking one flower from 25 plants of each morph. The pistil length, the length of one petal and the length of one petal notch (the difference between the petal length and the petal length to the base of the terminal notch) were measured. The averages for the three measurements were calculated for the two morphs of each sample.

The two morphs differ almost consistently in all three measurements (Table 5, Fig. 3 and 4). Yellow-centered flowers have longer petals in all 18 samples, longer petal notches in all but one sample of race *c*2, and shorter pistils in all but one sample of race *c*1 and one sample of race *c*2. Despite the differences between the two morphs and the variation between samples of the same race, the points for both morphs of a race tend to cluster, as shown in Fig. 4 and 5 and to separate from those of other races. That is, there are racial differences in the three measurements, which are often greater than the differences between morphs of the same

FIG. 2. Four flowers of one F_1 hybrid plant with variable flower color, from a cross between a yellow-centered plant of race *c*3 of *L. crassa* and a yellow plant of race *c*2. Note the variation between petals in pigment distribution, in the lower right flower.







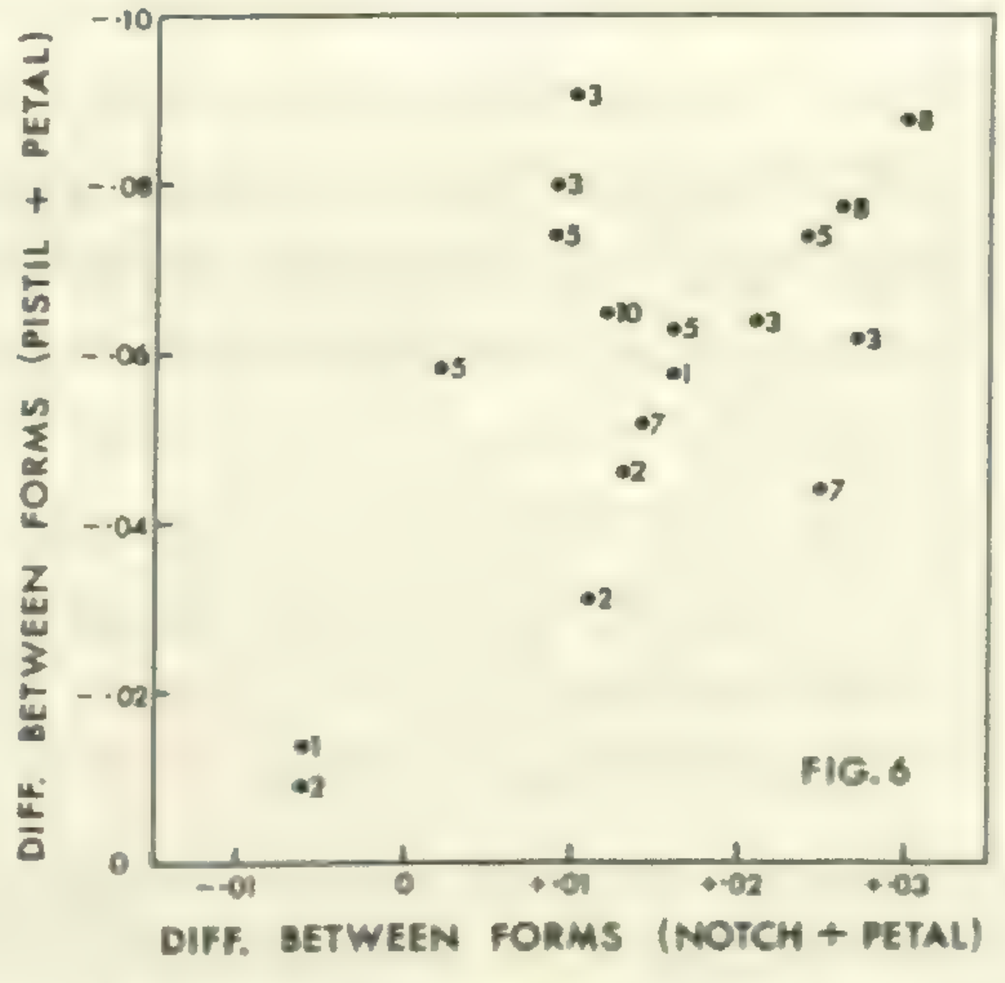


FIG. 3 to 6. Floral measurements and derived ratios of yellow and yellow-centered flowers in seven *L. crassa* races. In *Figs.* 3 to 5, lines connect the points for the morphs from the same collection; the figures, indicating the race, are beside the points for yellow flowers. In *Fig.* 6, the difference between yellow and yellow-centered flowers in petal notch length divided by petal length is graphed against the difference in pistil length divided by petal length. The point (0, 0) represents no difference between the morphs.

race. Races *c1* and *c2* have similar measurements in all three characters. Races *c3* and *c5*, which are morphologically very similar, are also indistinguishable in the three measurements.

There are, therefore, parallel differences between the morphs in the seven races, despite considerable evolution in the characters measured. Moreover, the genetical basis of yellow versus yellow-centered variation is different in the quasimorphic and polymorphic races. The morph differences in floral measurements probably represent pleiotropic effects of the alleles determining pigment pattern, rather than the effects of genes closely linked to the loci determining pigment pattern.

It is also apparent in Fig. 3 and 4 that the three measurements are positively correlated. To obtain characters which are independent of flower size, the average pistil length divided by average petal length, and the average notch length divided by average petal length were calculated for both morphs of each sample (Table 5). The pistil:petal ratio is consistently greater for yellow flowers than for yellow-centered flowers in all seven races. The notch:petal ratio is smaller for yellow flowers than for yellow-centered flowers in all but two of the samples—again, one sample of race *c1* and one of race *c2* are anomalous. When the two ratios are graphed against each other (Fig. 5) the points for a race again tend to separate from points for other races. That is, the differences between the morphs in the ratios are common to all races, although the ratios themselves vary considerably between races.

The differences between the morphs in the two ratios are graphed in Fig. 6. The races do not separate from each other completely, but it is apparent that the amount of the difference between the morphs also varies between races. The points for the quasimorphic races *c1* and *c2* are generally closer to the

TABLE 6. Average number of pollen grains in yellow and yellow-centered flowers of *L. crassa*

	Number of pollen grains × 1000			
Flower color	*Race c3 Popn. 37*	*Race c5 Popn. 58*	*Race c5 Popn. 100*	*Race c8 Popn. 72*
Yellow-centered	53.0	31.6	37.4	41.0
Yellow	43.8	29.4	35.0	25.2

origin than are the points for the polymorphic races. Thus the differences between yellow and yellow-centered flowers are less

in the quasimorphic races, although the flowers are larger in these than in the polymorphic races.

The average number of pollen grains per flower in five yellow and five yellow-centered flowers was estimated for four populations of the polymorphic races *c3*, *c5* and *c8* (Table 6). In all four populations, the average number of pollen grains was found to be higher in yellow-centered flowers than in yellow flowers.

The yellow and yellow-centered morphs in *L. crassa* differ in average measurements affecting three floral organs: the petals, pistils, and stamens, as well as in the pattern of petal pigmentation. There are, however, no consistent differences between the two morphs in the number of ovules per flower, anther length, or the percentage of successful self-pollinations (Lloyd, 1965 and unpublished thesis).

Number of Flowers

The number of flowers produced by naturally growing plants with yellow and yellow-centered flowers was compared in 13 samples, taken from nine populations of the closely related polymorphic races *c3* and *c5* of *L. crassa*. The samples consisted of 50 plants of both morphs taken from a transect across a population at the end of the flowering season. The average numbers of flowers produced by the two morphs and the combined average were

Table 7. The average and relative numbers of flowers produced by plants with yellow-centered and yellow flowers in samples from natural polymorphic populations

Race	*Year*	*Population no.*	*Nature of site*	*Average number of flowers*[1]			*Rel. no. flowers*
				Yellow-centered (1)	*Yellow (2)*	*Y-centered and yellow*	*Y-centered ÷ yellow (1) ÷ (2)*
c3	1961	61	glade	2.59	3.18	2.89	0.816
c3	1962	61	glade	3.00	3.74	3.37	0.802
c3	1962	37	pasture	5.68	5.24	5.46	1.084
c3	1962	89	glade	5.72	5.78	5.75	0.990
c3	1962	89	glade	6.66	8.10	7.38	0.822
c5	1961	70	roadside	8.28	7.28	7.78	1.138
c5	1961	36	pasture	8.97	8.88	8.92	1.010
c3	1961	89	glade	10.66	12.46	11.56	0.856
c5	1962	948	cornfield	14.34	14.98	14.66	0.957
c5	1962	944	cornfield	19.20	19.54	19.37	0.983
c5	1962	36	pasture	21.72	18.98	20.35	1.144
c5	1962	58	cornfield	28.68	21.28	24.98	1.348
c3	1962	88	cornfield	41.42	35.18	38.30	1.177

[1] The samples are listed in the order of increasing average number of flowers per plant.

calculated for each sample (Table 7). The samples were taken from a variety of habitats and the combined averages vary widely, from 2.89 to 38.30 flowers per plant.

The fruits of all plants of one morph in a sample were mixed together, so it is not possible to compare statistically the flower production of the morphs in a sample. The relative number of flowers produced by the morphs has been compared by calculating the number of yellow-centered flowers divided by the number of yellow flowers (Table 7). This varies from 0.80 to 1.35. Thus, there is no consistent difference between the morphs in flower production. But when the logarithm of the relative number of flowers is plotted against the logarithm of the average number of flowers per plant (Fig. 7), the points for the thirteen samples have a bivariate normal distribution and are significantly correlated ($r = +0.67$, $P = .02–.01$). The regression of the logarithm of the relative number of flowers (Y) on the logarithm of the average number of flowers (X) was calculated. When the plants produce an average of three flowers each (near the lower limit of the samples), the relative number of flowers, reconverted from logarithms, has an estimated average of 0.84, with 95 per cent confidence limits of 0.73 and 0.98. That is, plants with yellow-centered flowers produce significantly fewer flowers and the reduction is estimated to be 16 per cent of the flower production of the yellow morph. When the plants produce an average of 30 flowers each (near the upper limit of the samples), the average relative number of flowers is estimated at 1.16, with 95 per cent confidence limits of 1.02 and 1.38. That is, plants with yellow-centered flowers produce significantly more flowers than yellow-flowered plants and have an estimated advantage of 16 per cent of the flower production of the yellow morph.

In races *c3* and *c5*, therefore, under poorer growing conditions the yellow morph produces more flowers, but under more favorable conditions the yellow-centered morph produces more flowers. The estimates of the relative number of flowers suggest that the advantage of each morph under opposite extremes is considerable.

Insect Visits

Observations were made to determine whether the insects visiting *Leavenworthia* flowers are equally attracted to the most

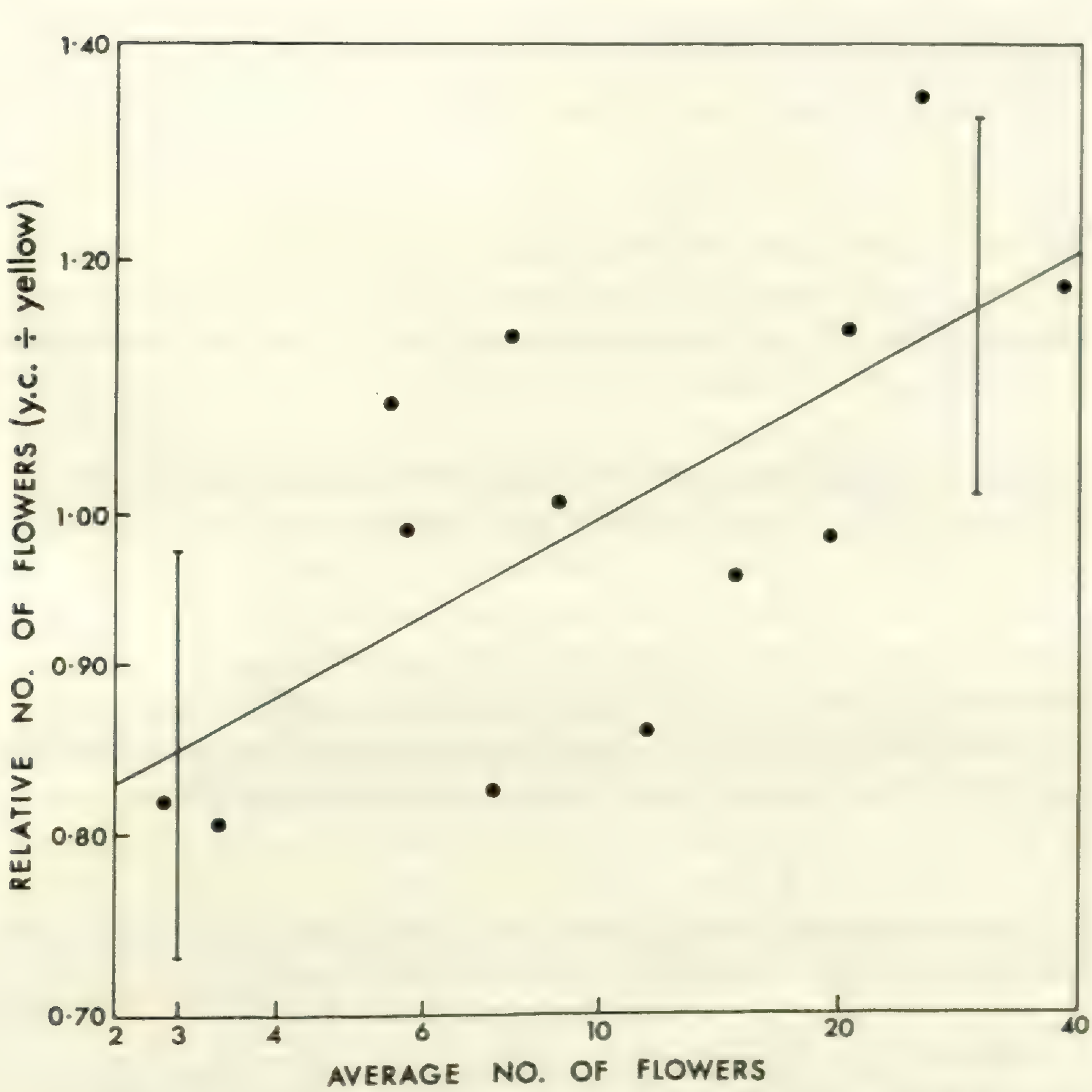


FIG. 7. Regression of the relative number of flowers produced by yellow and yellow-centered morphs (Y) on the average number of flowers produced by both morphs (X) in polymorphic populations of races *c3* and *c5* of *L. crassa*. The scale of both axes is logarithmic. The vertical lines show the 95 per cent confidence limits of $\bar{Y}$ when $X = 3.0$ and 30.0.

common petal colors, yellow, yellow-centered and eye-intermediate. The visits of insect species to the three morphs were compared with the frequencies of these morphs in four plots on two populations of the polymorphic race *c*3 of *L. crassa*. Population 89 occupied a pre-agricultural glade site in which the yellow-centered morph was more common than the yellow morph, and plants with eye-intermediate flowers were more common than in any other *Leavenworthia* population. Population 88 occupied an adjacent corn field in which yellow-flowered plants were most common, and plants with eye-intermediate flowers were absent. In both populations, the plants were small and rarely produced more than one or two flowers at a time, and the morphs appeared to be randomly dispersed.

Plots were marked out, by a string line between pegs, to form squares enclosing a thousand or more flowers. The frequencies of the flower colors were recorded in diagonal transects across the plots (Table 8). Insect visits to the morphs within a plot were recorded on the same day as the flowers were counted.

HONEY BEES: On both Populations 88 and 89, honey bees (*Apis mellifera* L.) were the most frequent flower visitors, comprising about 70 per cent of the insects on these populations in both 1961 and 1962. The percentages of their visits to the morphs are similar to the flower frequencies in the four plots. Considering yellow-

TABLE 8. The frequencies of morphs and of insect visits to the morphs in four plots

Plot Number	*Population and year*	*Flowers and insects*	*No. insect individuals*	*Total no. visits or flowers*	*Percentages of flowers and visits*		
					Yellow-centered	*Yellow*	*Eye-intermediate*
1	89, 1961	**Flowers**	–	**126**	**60.3**	**34.9**	**4.8**
		Honey bees	9	214	62.6	30.8	6.5
		Bombylius	5	185	94.1	4.9	1.1
2	89, 1962	**Flowers**	–	**588**	**74.7**	**23.0**	**2.4**
		Honey bees	9	353	74.2	22.7	3.1
		Solitary bee-1	5	168	73.2	21.4	5.4
		Solitary bee-2	5	162	74.1	23.5	2.5
		Solitary bee-3	4	79	70.9	24.1	5.1
		Sol. bee-total	14	409	73.1	22.7	4.2
		Bombylius	3	122	100.0	0.0	0.0
		Anthocaris	1	147	68.0	26.5	5.4
3	89, 1962	**Flowers**	–	**642**	**65.7**	**30.2**	**4.1**
		Honey bees	4	176	60.8	28.4	10.8
		Anthocaris	2	81	70.4	26.0	3.7
4	88, 1961	**Flowers**	–	**1031**	**41.8**	**58.2**	**0.0**
		Honey bees	1	60	40.0	60.0	0.0
		Bombylius	5	245	85.3	14.7	0.0

centered and yellow flowers only, the proportions of flowers and honey bee visits did not differ significantly in any of the four plots ($\chi^2<0.50$, $P>.05$ in all plots). The χ^2 tests can be combined by the relationship $d = \Sigma\chi/\sqrt{\text{d.f.}}$ (Simpson *et al.*, 1960), giving $d = 0.17$, $P>.05$. In contrast, the frequency of honey bee visits to eye-intermediate flowers exceeds that of the frequency of these flowers in all three plots containing this morph. The excess of visits to eye-intermediate flowers, compared with visits to yellow and yellow-centered flowers combined, is significant in Plot 3 ($\chi^2 = 10.81$, $P<.01$) and in the three plots combined ($d = 2.42$, $P<.01$).

SOLITARY BEES: Twenty species of solitary bees, the natural pollinators of *Leavenworthia* flowers, were collected on Populations 88 and 89 and nearby populations (Lloyd, 1965). These comprised about 15 per cent of the insect visitors to Populations 88 and 89. The visits of the three most common species were recorded in Plot 2 (Table 8). The proportions of visits to yellow and yellow-centered flowers are not significantly different among the three bee species ($\chi^2 = 0.02$, d.f. $= 2$, $P>.05$). Combining the counts from the three species, the relative number of visits to yellow and yellow-centered flowers did not differ significantly from the frequency of the flowers ($\chi^2 = 0.005$, $P>.05$). All three species visited eye-intermediate flowers in frequencies above that of the morph in the plot. The higher frequency of visits to eye-intermediate flowers is not significant ($\chi^2 = 2.52$, $P>.05$), but the total number of solitary bee visits recorded on eye-intermediate flowers was only 17.

DIPTERA: Eight Dipteran species were collected on *Leavenworthia* flowers in the vicinity of Populations 88 and 89. *Bombylius major* L., one of the most common of these, is the only fly species which moves from flower to flower rapidly enough for visits to the morphs to be counted. The visits of several *Bombylius* individuals were recorded on Plots 1, 2 and 4 (Table 8). *Bombylius* flies visit very few yellow flowers. In Plot 2, three individuals did not visit any yellow flowers, but in Plots 1 and 4 *Bombylius* individuals visited a few yellow flowers. The preference of *Bombylius* for yellow-centered instead of yellow flowers is highly significant in all plots ($\chi^2 = 48.28$, 34.10, 150.00 in Plots 1, 2 and 4 respectively, $P<.001$ in all tests). *Bombylius* also visited very few eye-intermediate flowers. The visits of *Bombylius* individuals to

yellow-centered and eye-intermediate flowers were compared with the flower frequencies by exact 2×2 contingency tests. The proportion of visits to eye-intermediate flowers was significantly below the proportion of the flowers themselves, in both Plot 1 ($P = .014$) and Plot 2 ($P = .034$). Thus *Bombylius* individuals favor yellow-centered flowers over both yellow and eye-intermediate flowers. This preference was noted on many occasions other than those of the exact counts described here, and seems to be a constant feature of *Bombylius* visits to polymorphic *Leavenworthia* populations.

No counts were made of the visits of other Diptera species *(Syrphidae* and *Stratiomyidae)* to the *Leavenworthia* morphs. But they appear to visit the morphs indiscriminately and certainly do not show a marked preference for yellow-centered flowers. LEPIDOPTERA: Several species of Lepidoptera occasionally visit *Leavenworthia crassa* flowers. The visits of the most common species, *Anthocaris genutia (Pieridae),* to the three morphs were recorded in Plots 2 and 3 (Table 8). Considering the yellow and yellow-centered flowers only, the relative numbers of the flowers and the visits of *A. genutia* did not differ significantly in either Plot 2 ($\chi^2 = 1.25$, $P > .05$) or Plot 3 ($\chi^2 = 0.48$, $P > .05$). Moreover, the relative numbers of eye-intermediate flowers and yellow plus yellow-centered flowers did not differ significantly from the relative numbers of *A. genutia* visits in either Plot 2 ($\chi^2 = 2.81$, $P > .05$) or Plot 3 ($P = 1.00$, since the frequencies of flowers and visits could not be closer). *A. genutia,* therefore, appears to visit the three morphs at random.

DISCUSSION

Within the limits described, the populations of a *Leavenworthia* race are similar in the kinds and frequency of the petal colors they contain. However, the spectrum of morph frequencies differs greatly between races. Many factors interact to determine racial differences in morph frequencies. These include breeding systems, environmental variation, allelic differences, pleiotropy or linkage relationships of the alleles and the genetic background.

The difference between races in morph frequencies may be due, in part, to the genes determining petal color. There is little information indicating whether a petal color is determined by the same

allele in different races. In *L. crassa*, yellow is dominant to yellow-centered in the quasimorphic races, but recessive to yellow-centered in the polymorphic races.

The incomplete dominance of the yellow and yellow-centered forms in crosses between races indicates that dominance relationships in each population are not intrinsic properties of the alleles, but depend on polygenic modifiers, which differ between races (cf., Harland, 1936; Clarke and Sheppard, 1963). The canalized developmental pathways, leading to one or another of the pigment patterns, are disturbed in the mixed genetic background of hybrids. The appearance, in the hybrids, of intermediate pigment patterns, similar to those occurring in natural populations, raises the question of the relationships of the intermediate patterns to the more common centered and uniform patterns. The results of progeny tests and crosses indicate that in *L. crassa* the intermediate patterns are produced by different alleles, and probably at a different locus, from the yellow versus yellow-centered variation. Moreover, in both quasimorphic and polymorphic races, the frequency of the intermediate morphs varies independently of the ratio of yellow to yellow-centered plants. These results suggest that the intermediate morphs are not directly involved in variation in the frequency of yellow and yellow-centered morphs, and that the resemblance between the intermediate hybrids and the naturally occurring intermediate patterns is fortuitous.

The breeding systems of the populations have had a pervasive effect on genetical variability at loci which determine flower color. The evolution of monomorphism from a polymorphic or quasimorphic condition has occurred in a number of phyletic lines, together with the evolution of characters facilitating self-fertilization. The loss of all but one morph in these races of *Leavenworthia* may be attributed to increased inbreeding (cf., Baker, 1953; Grant, 1958; Jain and Marshall, 1967).

The breeding systems can account for many of the racial differences in the numbers of morphs, but not which morphs are present or their frequencies. Moreover, few of the differences between races can be explained by environmental variation. Populations of the same race have similar morph frequencies, even when they occupy a diversity of habitats. Conversely, races with different morph frequencies occupy similar habitats.

In the yellow plus yellow-centered races of *L. crassa*, the poly-

morphism has persisted through the differentiation of five races, despite frequent self-fertilization and the small size of glade populations. In the quasimorphic races, the repeated occurrence of the rare petal colors in numerous populations indicates that they frequently persist for long periods in a population. Thus, in both quasimorphic and polymorphic populations, there is a balance of mutation and selective forces controlling the frequency of the alleles which determine petal color variation. Ford (1964) defined a polymorphism as "the occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation." If Ford's definition is applied strictly, almost all populations which have genetically determined discontinuities would be described as polymorphic. There is no non-arbitrary frequency for two forms beyond which they can be said to be polymorphic. However, in *Leavenworthia*, the distinction between the population structures of quasimorphic and polymorphic races can be recognized by defining a polymorphism as the occurrence of two or more discontinuous forms in intermediate frequencies in a population. A lower limit of three per cent for two polymorphic petal colors almost consistently separates the populations of quasimorphic and polymorphic races, and allows the two types of races to be conveniently distinguished. The recognition of a polymorphism, based on this definition, is arbitrary. However, it is the criterion generally used to decide whether or not the presence of two or more allelic forms in a population constitutes a polymorphism.

Some of the selective forces maintaining two alleles in intermediate frequencies in the yellow plus yellow-centered polymorphism in *L. crassa* are known. Differences between the morphs in flower production probably contribute toward the maintenance of the polymorphism, since flower production is a direct component of fitness, and the morphs are each favored under opposite conditions. In both glade and secondary populations, the size of the plants varies considerably throughout a population and from year to year (Lloyd, 1965). Disruptive selection for the two alleles may help to keep them both in a population, but the spatial and temporal heterogeneity of the environment is probably too erratic for this alone to maintain the polymorphism, especially in the small glade populations of the more inbred races.

There is no clear association between the size of the plants and morph frequencies in polymorphic populations. Glade populations usually have much smaller plants than populations on cultivated fields, but the yellow and yellow-centered morphs are equally common in both habitats. Two factors may prevent a close association between average plant size and morph frequency. The two morphs, and not the three genotypes, were compared in flower production. The numbers of flowers produced by the dominant homozygote and the heterozygote, which are phenotypically indistinguishable, may have a major effect on morph frequencies. Secondly, the spatial and yearly variations in plant size probably prevent uniform, stable equilibrium frequencies from being maintained throughout a population. In extreme cases, reductions in plant number and plant size in a population may allow random genetic drift in allele frequencies.

The relative flower production of the yellow and yellow-centered morphs may determine which of them has been selected in monomorphic races. In *L. crassa*, three yellow-centered races and three yellow races have a monomorphic condition which is probably derived from a previous polymorphism. In general, the monomorphic yellow-centered races are less well adapted to autogamy than the yellow races. Similarly, in *L. exigua*, the yellow-flowered var. *lutea* has a more advanced breeding system than the two races with yellow-centered flowers. In general, the more inbred races occupy poorer glade sites than those less well adapted to autogamy (Lloyd, 1965). The yellow-centered races may have become monomorphic under relatively favorable conditions, when the yellow-centered morph has a higher flower production. The monomorphic yellow races may have become so under harsher conditions which favor the yellow morph, and a regular inbreeding system of reproduction.

The visual appearance of the yellow and yellow-centered flowers does not seem to play an important role in maintaining the polymorphism, or in determining morph frequencies. The two color patterns appear to be equally attractive advertisements for bees, the only important pollinators of *Leavenworthia* flowers. However, the possibility exists that one or another morph may be preferred under other conditions than those prevailing when the counts were made. Bees may also visit a morph excessively when it is uncommon; the preference of bees for the infrequent

eye-intermediate flowers may contribute to the persistence of this morph in many populations. The preponderance of *Bombylius* visits to yellow-centered flowers is not an important factor controlling morph frequencies, since *Bombylius* is a minor visitor and an ineffective pollinator.

The differences between yellow and yellow-centered flowers in floral measurements are unlikely to have appreciable direct effects on the reproductive success of the morphs. They indicate, however, that the morphs differ in a number of physiological processes, either through pleiotropic action of the alleles or linkage to other loci, which may affect the relative fitness of the genotypes.

The yellow plus yellow-centered polymorphism of *L. crassa* races has persisted through the differentiation of five races in small glade populations whose plants are frequently self-fertilized. Regular inbreeding, genetic drift, and fluctuations in the relative flower production of the morphs would eventually lead to the fixation of one allele. There must be a selective force operating on the alleles which maintains them both under a variety of environmental conditions. Overdominance, at or near the loci responsible for petal color polymorphism in *Leavenworthia*, may explain the persistence of the two alleles in intermediate frequencies. Hayman (1953) has demonstrated that two alleles can persist in intermediate frequencies, in a population which reproduces by a mixture of self-fertilization and random mating, if the selection coefficients of the two homozygotes are not too dissimilar. Allard and coworkers (e.g., Jain and Allard, 1966) have explained persistent polymorphism in regularly inbreeding species on the basis of heterozygote advantage associated with segments of chromosomes.

The distribution and frequency of the morphs in *Leavenworthia* races cannot be fully explained by the results described above. But it is apparent that many factors interact to determine the floral diversity of *Leavenworthia* populations. The persistence of a polymorphism in some regularly inbreeding races, and the estimates of the relative number of flowers produced by the morphs, indicate that powerful selective forces are operating to maintain the polymorphism.

Summary

In natural populations of the 29 geographic races of seven *Leavenworthia* species, three pigments and four patterns of pig-

ment distribution are found in the petals. The range of frequencies of the petal colors (morphs) in each race is described, and three types of race are recognized—monomorphic, quasimorphic (one morph predominates and one or more additional morphs occur in low frequencies in some populations) and polymorphic (two morphs common in all populations). The number of morphs in a race tends to decrease as the adaptations to cross-pollination decrease and those to self-pollination increase; that is, genetical variability decreases as inbreeding increases. In polymorphic races of *L. crassa*, yellow flowers are recessive to yellow-centered flowers; in quasimorphic races yellow is dominant. In crosses between races, but not in crosses between plants of the same population, the yellow and yellow-centered morphs often show incomplete dominance. In one cross, some of the hybrid plants are variable in flower color.

In *Leavenworthia crassa*, yellow and yellow-centered flowers differ in average petal, petal notch and pistil lengths, and derived ratios and in the average number of pollen grains per flower. In polymorphic races of *L. crassa*, plants with yellow-centered flowers produce fewer flowers under adverse conditions, and more flowers under favorable conditions than yellow-flowered plants. The visits of several insect species to three morphs are compared with the frequencies of the morphs in natural polymorphic populations. Some insect species visit one or another petal color excessively, but this is probably not an important factor controlling morph frequencies.

The roles of breeding systems, flower production, and spatial and temporal heterogeneity of the habitat in determining morph frequencies are discussed. None of the known selective forces adequately explain the persistence of polymorphism in small inbred populations. Overdominance, at or near loci controlling polymorphic variation, may maintain the polymorphism.

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Literature Cited

Baker, H. G. 1953. Race formation and reproductive method in flowering plants. Symp. Soc. Exp. Biol. 7: 114-145.

Clarke, C. A. and P. M. Sheppard. 1963. Interactions between major genes and polygenes in the determination of the mimetic patterns of *Papilio dardanus*. Evolution **17**: 404-413.

Daday, H. 1965. Gene frequencies in wild populations of *Trifolium repens*. IV. Mechanism of natural selection. Heredity **20**: 355-365.

Epling, C., H. Lewis and F. M. Ball. 1960. The breeding group and seed storage: a study in population dynamics. Evolution **14**: 238-255.

Ford, E. B. 1964. Ecological Genetics. Methuen and Co., London.

Grant, V. 1958. The regulation of recombination in plants. Cold Spring Harbor Symp. Quant. Biol. **23**: 337-363.

Harland, S. C. 1936. The genetical conception of the species. Biol. Rev. Camb. Phil. Soc. **11**: 83-112.

Hayman, B. I. 1953. Mixed selfing and random mating when homozygotes are at a disadvantage. Heredity **7**: 185-192.

Heslop-Harrison, J. 1964. Forty years of genecology. Advances in Ecological Research **2**: 159-247.

Hovanitz, W. 1953. Polymorphism and evolution. Symp. Soc. Exp. Biol. **7**: 238-253.

Huxley, J. S. 1955. Morphism and evolution. Heredity **9**: 1-52.

Jain, S. K. and R. W. Allard. 1960. Population studies in predominantly self-pollinated species. I. Evidence for heterozygote advantage in a closed population of barley. Proc. Nat. Acad. Sci. **46**: 1371-1377.

Jain, S. K. and D. R. Marshall. 1967. Population studies in predominantly self-pollinated species. X. Variation in natural populations of *Avena fatua* and *A. barbata*. Amer. Natur. **101**: 19-33.

Jones, D. A. 1966. On the polymorphism of cyanogenesis in *Lotus corniculatus*. I. Selection of animals. Canad. Jour. Genet. and Cytol. **8**: 556-567.

———————. 1967. Polymorphism, plants and natural populations. Science Progress **55**: 379-400.

Joshi, B. C. and S. K. Jain. 1964. Clinal variation in natural populations of *Justicia simplex*. Amer. Natur. **98**: 123-125.

Lloyd, D. G. 1965. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). Contr. Gray Herb. **195**: 3-134.

New, J. 1958. A population study of *Spergula arvensis*. I. Two clines and their significance. Ann. Bot. (N.S.) **22**: 457-477.

Rollins, R. C. 1963. The evolution and systematics of *Leavenworthia* (Cruciferae). Contr. Gray Herb. **192**: 1-98.

Simpson, G. G., A. Roe and R. C. Lewontin. 1960. Quantitative Zoology. Harcourt, Brace and Co., New York.

THE GENUS KALLSTROEMIA (ZYGOPHYLLACEAE)

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My interest in the *Zygophyllaceae* dates from 1959 (at Stanford University), when I began a taxonomic study of the family as it occurs in Baja California, Mexico. As I became more familiar with the family, it became increasingly obvious that the genera under investigation were badly in need of taxonomic revision, although their species in Baja California were relatively distinctive. I chose to study *Kallstroemia* because it appeared to be the New World genus most in need of revision. In addition, it is the largest genus of the *Zygophyllaceae* in the New World, elsewhere being surpassed in number of species only by *Fagonia*, *Tribulus*, and *Zygophyllum*.

Such statements as: "Será necessario hacer una revisión minuciosa de las especies centro y norteamericanos para establecer el valor de ellas." (It will be necessary to do a thorough revision of the Central and North American species in order to establish their validity.) (Descole, *et al.*, 1939, p. 221); "There is some difference of opinion as to how the species of this genus should be defined, and the characters for separating them are usually rather vague and unsatisfactory." (Standley & Steyermark, 1946, p. 397); and ". . . revision of the genus is needed." (Macbride, 1949, p. 397), showed a realization of the need for revision. In the following study, I have attempted to do my part in reducing the taxonomic chaos hitherto present in *Kallstroemia*.

The conclusions arrived at are based on the examination of herbarium specimens, and the collection and field observation of about half the species. The observations of wild populations throughout much of the range of the genus have yielded valuable information. In addition, four of the species were studied in greenhouse plantings, which provided information as to seed germination, seedling morphology, and compatibility relationships involving the breeding system.

At the beginning of the investigation, it was planned to obtain chromosome numbers for as many of the species as possible, and to attempt crossing experiments between different species. Unfortunately, these goals proved to be impossible to achieve, be-

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cause most of the preserved cytological material did not contain the requisite meiotic stages. In addition, there was an inadequate amount, and only sporadic flowering, of the greenhouse material. Chromosome numbers for species of the genus remain unknown, as no countable configurations were found in approximately 250 field collections of buds examined for meiosis.

Although morphological analyses provided a basis for interpreting certain natural relationships between the species, the information at hand is not adequate to provide more than the barest outline of phylogenetic relationships within the genus. Future studies utilizing additional field observations, breeding experiments on a large scale, and information regarding chromosome numbers, while perhaps not changing the basic concepts regarding the species of the genus, undoubtedly will permit a more natural classification of *Kallstroemia* than is given in the present work.

GENERIC RELATIONSHIPS

The most recent synopsis of the *Zygophyllaceae* (Scholz, 1964) follows Engler's (1890, 1915, 1931) placement of *Kallstroemia* in the tribe *Tribuleae* Rchb. of the subfamily *Zygophylloideae* along with *Kelleronia* Schinz, *Neoluederitzia* Schinz, *Sisyndite* E. Mey. ex Sond., and *Tribulus* L. Engler (1931) further divided the *Tribuleae* into two subtribes, the *Neoluederitziinae* Engl. (including *Neoluederitzia* and *Sisyndite*) and the *Tribulinae* (with *Kallstroemia, Kelleronia,* and *Tribulus*). These five genera were considered to be closely related and to have arisen from a "single primitive stock" (Engler, 1915, 1931). Comparative morphology and palynology, however, indicate that whereas *Kallstroemia, Kelleronia,* and *Tribulus* form a natural group, *Neoluederitzia* and *Sisyndite* have affinities elsewhere in the family.

In addition to the differences segregating the *Tribulinae,* stated by Engler and others (e.g., herbs versus shrubs or trees; indehiscent mericarps versus dehiscent capsules; lack of endosperm versus its presence; lack of staminal appendages versus their presence), pollen grain morphology has been utilized more recently as an additional criterion of separation. Descole, *et al.,* (1940) were the first to distinguish the *Tribuleae* from the *Zygophylleae* on the basis of polyforate versus tricolporate pollen,

and Erdtman (1952) and Agababian (1964), in surveys of pollen grain morphology in the family, have indicated the homogeneity of the *Tribulinae* and the lack of similarity to the rest of the family. The latter author concludes (p. 44) that, "the determination of the relationships of this group of genera appears to be difficult" [translation by Dr. G. K. Brizicky].

Another genus that should be included in this assemblage is *Tribulopis* R. Br., which some consider to be a synonym of *Kallstroemia,* while others include it in *Tribulus. Kallstroemia, Kelleronia* and *Tribulopis* have each, at one time or another, been considered synonyms of *Tribulus,* but there is good evidence supporting their position as separate genera, which constitute a natural group deserving recognition as a major subdivision of the family.

Kallstroemia is composed of 17 species native to the New World: *Kelleronia* has about ten species in Ethiopia, the Hadhramaut, and Somaliland; *Tribulopis* some half-dozen species in tropical and subtropical Australia; and *Tribulus* a number of species native to the Old World. Like most members of the family, they are to be found mainly in arid and semiarid areas.

Specimens of *Tribulopis* and *Tribulus,* as well as *Kallstroemia,* have been examined morphologically and anatomically. However, no material of *Kelleronia* has been seen. Morphological details of the latter genus have been taken from Schinz (1895), Baker (1898), Engler (1915, 1931), Chiovenda (1916, 1917, 1929), Erdtman (1952), and Agababian (1964).

These four genera differ from other *Zygophyllaceae* in that they are mostly prostrate to ascending annual herbs, with opposite, even-pinnate leaves and inequilateral, ovate (rarely linear) leaflets. They have ten stamens with unappendaged filaments in two unequal series, and each filament of the outer whorl is adnate at the base to the basal portion of the petal opposite. Nectariferous tissue is present between the stamens and perianth, pollen is polyforate, and they all have indehiscent mericarps. Vegetatively, the members of this alliance are rather similar, differing mainly in details of flowers and fruits.

The five sepals are herbaceous, more or less ovate, concave, pubescent, and scarious-margined in all, deciduous in *Kelleronia, Tribulopis,* and *Tribulus,* being persistent in all species of *Kallstroemia* except *K. californica.* The five petals are free, white

to orange, obovate to truncate, as long as to longer than the sepals, prominantly veined, and hemispherically spreading. They are marcescent only in *Kallstroemia.*

All four genera have five bilobed, nectariferous glands between each of the inner whorl of stamens and the sepals. These glands project downward and outward between the adjacent petals into the concave sepal base. In addition, *Tribulopis* and *Tribulus* have a second whorl of nectaries between stamens and ovary opposite the outer whorl of stamens. It is unknown whether *Kelleronia* has this second set of nectaries, but they are absent from *Kallstroemia.* In *Tribulus,* the interior nectaries are triangular and free [*T. alatus* Del., *T. macropterus* Boiss., *T. terrestris* L. (Schweickerdt, 1937)], or connate into a five-lobed urceolate ring surrounding the base of the ovary [*T. cristatus* Presl, *T. excrucians* Wawra, *T. pterocarpus* Ehrenb., *T. pterophorus* Presl, *T. zeyheri* Sond. (Schweickerdt, 1937); *T. cistoides* L. (Brown, 1938)]. They are bilobed and connate at the base in *Tribulopis solandri* R. Br.

The ovary is five-carpellate in the four genera and is five-lobed and five-loculed in *Kelleronia, Tribulopis,* and *Tribulus.* In *Kallstroemia* it is ten-lobed and ten-loculed. Locule number is mirrored by the style and stigma, both being respectively five-ridged and five-lobed in *Kelleronia, Tribulopis,* and *Tribulus,* and ten-ridged and ten-lobed in *Kallstroemia.*

There is a single ovule per locule in *Kallstroemia* and *Tribulopis,* while *Kelleronia* has two or more, and *Tribulus* has two to five, arranged in two vertical rows on the placentae. In the two latter genera, each locule becomes two- to five-compartmented through the formation of transverse septae between the ovules. Therefore, in all four genera the ovules originally are pendulous, but ontogenetically they become horizontally arranged one above the other in *Kelleronia* and *Tribulus.* Consequently, *Kallstroemia* forms ten one-seeded mericarps, *Tribulopis* five one-seeded mericarps, and *Kelleronia* and *Tribulus* five two- to five-seeded mericarps in which the seeds are separated by transverse partitions. In *Kelleronia* and *Tribulus* the seeds are depressed and nearly horizontal, while those of *Kallstroemia* and *Tribulopis* are pendulous and obovoid. The number of seeds formed has been used in the separation of *Tribulopis* from *Tribulus,* but abortive ovules, resulting in reduced seed formation, are present in species of both these genera and in *Kallstroemia,* and probably result from inadequate pollination.

When the mericarps separate in *Kallstroemia*, they leave a persistent, styliferous axis that is topped by the persistent style, which forms a beak on the fruit. In *Tribulus* this axis is absent, and the style does not persist. It does persist to form a beak on the fruit of *Tribulopis*, but whether it does so following separation of the mericarps is unknown. Likewise, the situation in *Kelleronia* is unknown.

Virtually nothing is known of the reproductive biology of *Kelleronia* and *Tribulopis*, but there are some basic differences between *Kallstroemia* and *Tribulus*. In *Kallstroemia* individual flowers open for only a part of one day. Pollen and the stigma mature simultaneously. The petals are marcescent and fold convolutely together around the style following anthesis, appressing the anthers to the stigma and effecting self-pollination in all species but *K. perennans*. In *Tribulus*, flowers usually last about two days. *Tribulus cistoides* is protandrous (Robertson & Gooding, 1963), with pollen shed the first day and the stigma receptive the second, while *T. terrestris* is protogynous (Goldsmith & Hafenrichter, 1932), with the stigma receptive the first day and pollen shed the second. Self-pollination may take place, and it occurs most frequently by the stamens curving upward and appressing their anthers to the stigma unaided by the petals. It is probable also that insects aid in some selfing.

Certain differences in seed germination are found between *Kallstroemia* and *Tribulus*. In the former, germination is epigeal, the entire mericarp being carried upward by the expanding cotyledons. In *Tribulus* the cotyledons force their way upward to above ground level, but the mericarp remains in the ground. Usually only one seed germinates, but more than one may do so in some cases (Johnson, 1936). Cotyledons in *Kallstroemia* are bright green, simple, entire, concave on the abaxial surface, and have three well-marked palmate veins. They are ovate in outline and pubescent. Those of *T. cistoides* and *T. terrestris* differ in being rectangular, shiny-green, slightly tinged with yellow, parallel veined and glabrous.

It can be seen from the above discussion that evidence from comparative morphology supports the recognition of four genera in this alliance. However, evidence for the elucidation of phylogenetic relationships is lacking. More information is needed regarding the morphology of *Kelleronia*, and cytological and genetical data are needed before one can knowingly discuss the

natural relationships of *Kallstroemia, Kelleronia, Tribulopis,* and *Tribulus.*

MORPHOLOGY

This section contains a general review of vegetative, floral, fruit, and seed morphology in *Kallstroemia.* A more detailed comparison of morphological differences between species will be found in the section titled morphological characters and taxonomic criteria.

Vegetative Morphology

Habit. The diffusely branching herbaceous to suffrutescent stems of *Kallstroemia* spread radially from a stout, annual (perennial in *K. boliviana* and *K. perennans* and perhaps occasionally so in *K. hintonii* and *K. rosei*) root and branch primarily from the basal nodes. In most species, stems are prostrate to decumbent in mature plants, but in *K. grandiflora, K. parviflora,* and *K. perennans* they may be ascending. Stems of seedlings and young individuals of most species also are upright at first, but they soon fall over from their own weight and become prostrate or decumbent. Occasional individuals of *K. grandiflora* growing under exceptionally favorable conditions (e.g., along roadsides and in low places where rainwater has collected) may reach a height of one meter and a diameter of several meters. Size ranges from these large globose individuals of *K. grandiflora,* which may cover 16 square meters or more (Cannon, 1911), down to prostrate plants of *K. curta* and *K. hirsutissima* with a diameter of one to two feet.

Roots. The root system consists of a thick, fibrous, deeply penetrating, conical tap root with a relatively stout crown, that may reach a length of several decimeters. The slender, filamentous lateral roots are mainly parallel and close to the soil surface. In the Sonoran Desert near Tucson, Arizona, Cannon (1911) found that roots of *Kallstroemia grandiflora* may penetrate as deeply into the ground as those of some perennials in the same area, with the tap root reaching a length of 22 centimeters, and the longest lateral root being over 21 centimeters long. This deeply penetrating root system enables *Kallstroemia* to resume growth following

the normal growing season if an unseasonal rain should occur before the plant succumbs during the dry season.

Stems. Stem growth is sympodial, the apical meristem changing from a vegetative to a floral meristem at each successive node. Therefore, a flower terminates the stem, further growth taking place from a vegetative bud in the axil of one of the pair of leaves at the last node. This new stem axis crowds the terminal flower of the preceding axis aside, so that the stem has a characteristic zig-zag appearance with seemingly axillary flowers on alternate sides at the usually more or less swollen nodes. Branching occurs when the axillary bud of the opposite leaf grows out as well. This type of growth is characteristic of the *Zygophyllaceae* (Engler, 1890).

When fresh, the stems are terete, somewhat succulent, flexible, fibrous, and tough. Upon drying, they shrink in diameter and become brittle and striate, the striations being outward manifestations of a ring of cortical fibers. They are green, yellow-green, or reddish, drying to yellow.

Like the foliage, the stems usually are densely covered with unbranched, white, gray, or yellow nonglandular trichomes. These are unicellular outgrowths of epidermal cells which may be bulbously swollen basally. They are especially prevalent at the nodes. Trichomes are appressed toward the stem apex and usually also spreading in all species except *Kallstroemia peninsularis* and a few individuals of *K. pubescens* from Peru, where they are retrorse. There is a correlation between amount, but not type, of pubescence and various climatic and edaphic factors. The specimens from drier situations are the most pubescent, while at the other extreme individuals growing under mesophytic conditions are almost glabrous. Also, specimens from alkaline soils are much more pubescent than the average.

Stipules. A pair of free stipules is found on the stem at the base of the petiole. They are foliaceous, ciliate, persistent, narrowly to broadly falcate, acuminate, erect or spreading from the stem, and shorter than the petioles. The pubescence is the same as that on the stems.

Leaves. Vernation is imbricate, and the leaves are opposite, one of each pair alternately smaller than the other or sometimes abortive. They are slightly succulent and abruptly even-pinnate, with the petioles usually shorter than the leaflets. Seedling leaves

are less divided than those of the mature plant and grade gradually into them. Both petiole and rachis have the same type of pubescence as the stem, and the rachis is terminated by a foliaceous, subulate, pubescent, and apiculate mucro about one millemeter long.

Leaflets vary in number from two to ten pairs. They are usually somewhat unequal in size, those on one side of the rachis being slightly smaller than the other. The basal pair are markedly unequal, and the terminal pair more falcate and pointed forward than the lower pairs. The leaflets are opposite, basally oblique to inequilateral, entire, acute to obtuse, mucronate, apiculate, pubescent to glabrate, ciliate, and their margins may be flat or inrolled. Venation is reticulate.

Pubescence varies from heavy (especially on younger leaflets) to almost glabrate. Trichomes are similar to those on the stem. They are appressed toward the leaf apex and are found on both abaxial and adaxial surfaces of the blade and along its margins, being more numerous on the abaxial surface. Marginal trichomes may be so profuse as to give leaflets a whitish outline. Likewise, the petiole and rachis usually appear whitish because of numerous trichomes.

The leaves show marked nyctotropic movements, the leaflets rising soon after dark and adpressing their adaxial surfaces together. They return to their normal horizontal position before dawn. This movement is also readily observable within a short time after the plant is pulled from the ground. Nyctotropic movements have been observed to occur in all species of *Kallstroemia* grown in the greenhouse (*K. grandiflora*, *K. maxima*, *K. pubescens*, and *K. rosei*), and also in *Tribulus cistoides* and *T. terrestris*. Under very hot and dry conditions, the leaves will fold up during the day.

Floral Morphology

Peduncles. The peduncles are pseudo-axillary, shorter to longer than the leaves, more or less thickened distally (becoming more so in fruit), and have the same type of pubescence as the stems and leaves. They are reflexed in bud, and erect during anthesis. Following anthesis, they usually elongate and recurve under the leaves, becoming curved, straight, or sharply bent at the base and straight above.

Flowers. Flowers are solitary, pentamerous (occasionally hex-

amerous in *Kallstroemia tribuloides*), polypetalous, syncarpous, perfect, regular, and hypogynous. They appear to be alternate, but through sympodial branching of the stem they are borne terminally. Because of this seemingly alternate arrangement, the genus has been described as having a cincinnus as an inflorescence, but this is not the case. The flowers occasionally have been described as being tetramerous, but specimens of this type have not been seen.

Calyx. The five sepals are imbricate in bud. They are concave, free, lanceolate to broadly ovate in flower, foliaceous, pubescent, acute, apiculate, scarious margined, and inserted at the base of the receptacle. Trichomes may be the same or different from the type on the vegetative parts. They are not found on the scarious margins, but only on the green central portion of the abaxial surface, and occasionally on the adaxial surface. However, sepal margins usually appear ciliate, because the scarious margins nearly always fold involutely inward following anthesis, whether the remainder of the sepal does so or not. After anthesis the sepals may appear subulate or linear-lanceolate due to the involutely inward folding of their margins. They are persistent in all species except *Kallstroemia californica.*

Corolla. The five petals are convolute in bud. They are free, alternate with the sepals, elliptical to broadly obovate, rounded or truncate, and irregularly notched to entire at the apex, glabrous, as long or usually longer than the sepals, fugaceous, and usually marcescent. They have prominent veins, spread hemispherically, and are inserted at the base of a fleshy, obscurely ten-lobed disc. At the base, each petal is adnate to the base of the filament of the stamen in the outer whorl opposite it. Petal color varies from white through yellow to bright orange, and also may be basally green to red, the base being darker than the remainder of the petal.

Androecium. The androecium is obdiplostemonous, there being two whorls of five stamens each. Filaments are inserted in the disc; they usually are filiform to subulate, but are winged at the base in *Kallstroemia hintonii.* Those of the two whorls are of different lengths, the ones opposite the petals being longer than the inner whorl, but shorter than the petals. Filaments are the same color as the base of the petal, varying from green to red. They are generally long enough to reach the top of the style, but in *K. perennans* they are only about two-thirds the length of the

style. The connectives often contain druses that are presumably composed of calcium oxylate. Between the base of each filament of the inner whorl and the opposite sepal is a small, ovoid, bilobed nectary. It projects downward and outward between the bases of the adjacent petals into the concave sepal base.

The anthers are globose to ovoid or occasionally linear, yellow to red, bilobed, bilocular, tetrasporangiate, sub-basifixed to versatile, introrse, and longitudinally dehiscent. Those of the inner whorl occasionally are small and sterile.

The pollen grains are spherical, yellow to red, and have a polyforate exine. They are shed singly.

Gynoecium. The superior, sessile, ten-lobed, ten-loculed, globose to ovoid or occasionally conical ovary is glabrous to sparsely or densely pubescent with straight to curved, white or gray, unicellular trichomes. Placentation is axile, and the ovules are one per locule, pendulous, and anatropous, with a superior micropyle. Sometimes one or more is abortive, especially in individuals which have been self-pollinated.

The gynoecium has been described as five-carpellate, with two ovules per carpel which spuriously are divided in ontogeny by a vertical septum, thus only being secondarily ten-loculed with a single ovule per locule (Wight & Arnott, 1834; Torrey & Gray, 1838). However, ten locules are present throughout the growth of the ovary, and the change to this condition is not only ontogenetical, but is an evolutionary culmination of a phylogenetical trend.

The style arises from the summit of the ovary and is cylindrical or conical, with a more or less conical base. It varies from glabrous to variously pubescent, is more or less ten-ridged, and terminates in as many stigmatic bands as there are locules. It persists to form a beak on the mature fruit.

The clavate to capitate stigma is papillose (coarsely pubescent in *Kallstroemia perennans*), silvery, simple and basally lobed, or with distinct ridges. In *K. peninsularis* the stigmatic surfaces extend downward almost to the base of the style, but in all other species the stigma is terminal.

Fruit and Seed Morphology

Fruit. The fruit is a ten-lobed, glabrous or variously pubescent, ovoid or occasionally conical to pyramidal capsule which, upon

maturation, septicidally divides and separates into ten unilocular, one-seeded mericarps. However, there may be fewer than ten through abortion of some ovules. Both the beak (the persistent style) and the styliferous axis persist on the peduncle following this separation.

Mature mericarps are hard and nut-like, obliquely triangular, broadly wedge-shaped, and vary from whitish to black. The glossy, variously pitted lateral faces slope into a thin straight, curved, or angled adaxial edge. The abaxial surface is rounded and thicker, may be slightly keeled or cross-ridged, and usually bears a series of rounded to elongate tubercles. This surface varies from thickly pubescent to glabrous.

Seed. The oblong-ovoid seed is obliquely pendulous from the apex of the central angle of the mericarp and lacks endosperm. The testa is smooth, white, and membranaceous. It completely surrounds the embryo at maturity and is free from the mericarp wall.

The embryo is straight, with ovoid, foliaceous cotyledons, a superior, conical radicle, and a rudimentary epicotyl. The only information concerning embryology in the genus is Mauritzon's (1934) observation in "*Kallstroemia maxima*" that the suspensor consists of a single row of cells.

REPRODUCTIVE BIOLOGY

This section discusses general aspects of flowering, pollination, and seed germination in the genus. An account of suspected interspecific hybridization will be found in the section on interspecific relationships.

Flowering

Prior to anthesis, the peduncle in *Kallstroemia* is reflexed, with the developing bud lying beneath the herbage. As the flowering period is approached, it becomes erect, carrying the bud into an upright position. Following pollination, the peduncle elongates and usually once more becomes reflexed, forcing the developing fruit back below the leaves. This takes place in a single day.

Pollen is fully formed by the time the bud is about one millimeter in diameter, when the anthers are essentially still sessile

and before filament elongation has taken place. Meiosis in the microsporocyte is of the simultaneous type, no wall forms after the first division and the two divisions are almost simultaneous. Therefore, four free nuclei are found in the microsporocyte protoplast before cytokinesis takes place. This is followed in the developing pollen grains by the formation of a tetrahedral tetrad. The microsporocyte cell wall disappears late in pollen maturation, and the polyforate nature of the grains can be seen prior to the disintegration of this wall.

By the time the pollen grains are fully formed, the petals still consist only of primordial bumps on the receptacle. Their principal period of growth takes place after the anthers reach mature size. Both the petals and filaments accelerate their growth rate immediately prior to anthesis, exceeding the sepals only at this time.

Flowers in most species usually open only in the morning, closing about midday, except in cloudy weather, when they open later or remain closed. Flowering is accomplished by the convolute petals unfolding, spreading hemispherically, and forcing the sepals backward.

Sloane (1696, 1707), Don (1831), and Macfadyen (1837) have commented on the floral fragrance of *Kallstroemia maxima*. However, I have not detected any odor in the flowers myself. This trait is not reported for any other species of the genus.

Pollination

Species of *Kallstroemia* so far examined in the field or grown in the greenhouse are not self-pollinated prior to anthesis. Pollen is shed after the flower has opened, at which time the stamens are appressed to, or very near the spreading petals, and the stigma is held erectly above them. The stigma is receptive to pollen at this time. Although the stamens are differentiated into two series, the anther size is only exceptionally different in the two whorls, and all ten anthers dehisce more or less simultaneously.

The genus appears to be one which is pollinated promiscuously, being visited by various Diptera and Hymenoptera for pollen, and by these and Lepidoptera for nectar. Very few reports of the types of insects visiting the flowers have been recorded. According to notations accompanying herbarium specimens, *Kallstroemia*

grandiflora is visited by "bees and wasps" in Sonora and Colima, Mexico, and *K. maxima* by "honeybees and small flies" in Costa Rica. In Jamaica the latter species is sought out by small butterflies for its nectar.

The only pollinators of *Kallstroemia* to have been positively identified are bees of the genus *Perdita*, usually found in the deserts of the southwestern United States and northwestern Mexico on various *Compositae*. *Perdita pectidis* has been taken from "*Tribulus maximus*" (*Kallstroemia californica* or *K. parviflora*) in New Mexico (Cockerell, 1896). *P. echinocacti* has been found a number of times on *K. grandiflora* in Arizona and Sonora (Timberlake, 1954, 1960), and *P. euphorbiae* is known from the same species in Sonora (Timberlake, 1960).

When a honeybee lands on a flower of *Kallstroemia maxima*, it thrusts aside the stamens, while standing over them and the style in order to reach the nectar at the bases of the sepals. In this way pollen is transferred from the anthers to the bee, and from the bee to the stigma. The bee circles clockwise on the flower until it has sampled all the nectaries, then moves on to another flower, not uncommonly returning later to the original flower, either to repeat the previous performance or to reject the flower. The bee, therefore, may act not only as an agent in cross-pollination, but also may effect self-pollination by transferring pollen from anthers to stigma in the same flower. This is accomplished in either the initial visit or upon return of the bee to a flower previously visited.

Self-pollination also takes place through the following novel method. During the flowering period the filaments slowly curve upward, moving the anthers upward and appressing them to the style and stigma just before the petals close, which further appresses the anthers to the stigmatic surface. The clockwise, convolute twisting of the petals around the style as they close helps insure self-pollination in the absence of insect visitors. Although the petals are fugaceous, they usually are marcescent also and may persist twisted around the style until the fruit is mature. Greenhouse plantings of *Kallstroemia grandiflora*, *K. maxima*, *K. pubescens*, and *K. rosei* all have exhibited this phenomenon, and they have set seed following it as well. Most of the remaining species display this behavior also, for herbarium specimens of all species but *K. perennans* have revealed anthers appressed to stigmas and marcescent petals. In *K. perennans* the stamens are

only two-thirds as long as the style and do not reach the stigma, and the petals are fugaceous but not marcescent. The only other member of the *Zygophyllaceae* known to be self-compatible is *Larrea tridentata* (DC.) Cov. (Raven, 1963).

Seed Germination

Seeds of *Kallstroemia* are viable for at least three years, and Ernst (1876) claimed that seeds of *K. maxima,* among those of other weeds, retained their viability after having lain dormant in the soil for more than 30 years. However, there is some question as to whether the seeds were acually *in situ* for such a time, or whether they were introduced later upon exposure of the surface during excavation of the area in Caracas, Venezuela, where his observations were made.

Germination of the seeds proved difficult when mericarps were placed on moist filter paper in petri dishes and these placed in the dark at room temperature. Even if the mericarp wall was broken, germination was virtually nil. These mericarps also were more liable to fungal attack than those planted in three-inch pots in a 1:1 mixture of loam and peat-moss. Here the percentage of germination was high, regardless of whether the mericarp wall was broken or not. The percentage of germination was much lower for mericarps placed in pure sand, probably because it dried out much faster than the above mixture.

Germination takes place through the abaxial surface of the mericarp, which splits vertically down the center. It is epigeal, the entire mericarp being carried up into the air by the unfolding cotyledons. Following germination, rapid elongation of the primary root takes place, with the aerial parts growing more slowly. The first leaves, other than the cotyledons, have two pairs of leaflets, and a gradual increase in leaflet number takes place until that of the mature plant is reached. Flower buds generally begin to appear with the fifth or sixth leaf.

The pattern of germination exhibited by *Kallstroemia maxima, K. pubescens,* and *K. rosei* in greenhouse plantings is that termed "intermittent" by Salisbury (1961). Here the seeds germinate at irregular intervals. Following an initial burst of germination during the second week after the mericarps had been sown and first watered, seeds of a given planting were still intermittently

germinating over one year later. This pattern was independent of whether or not the mericarp wall had been broken, although seedlings from scarified mericarps did begin to sprout on the ninth day following planting, one day before those from non-scarified mericarps.

According to Salisbury, intermittency is frequently caused by diversity in the permeability of the seed coat. Whether this is true for *Kallstroemia* can be determined only through further experimentation. Another possible explanation is that growth inhibitors may be present in the seed coat or mericarp which must be leached out by rainwater or soil moisture. A water-soluble inhibitor of germination has been found in the fruit wall of *Zygophyllum dumosum* Boiss. (Koller, 1955), and the seeds of *Larrea tridentata* (Runyon, 1930) and of *Tribulus terrestris* (Johnson, 1936) exhibit dormancy, a phenomenon frequently caused by growth inhibitors (Evenari, 1949).

DISTRIBUTION AND ECOLOGY

Fossils of plants purported to belong to the *Zygophyllaceae* have been reported a number of times in the literature. However, with the exception of a single instance, all of these fossils are of extant shrubby genera with no discernable close relationships to *Kallstroemia*. The exception (Martin, 1963) is a report of pollen of *Kallstroemia* itself from southeastern Arizona, southwestern New Mexico, and northeastern Chihuahua. All of the localities from which *Kallstroemia* pollen was reported were alluvial deposits of less than 10,000 years of age. Unfortunately, the only information this gives us is that the genus was present at that time in an area in which it is still to be found.

Spatial Distribution

There are four species of *Kallstroemia* in North America that, with justification, can be termed primarily of the warm desert, even though three of them also occur outside the desert proper. These four species are *Kallstroemia californica*, *K. grandiflora*, *K. hirsutissima*, and *K. perennans*. The first three may at times be found growing in the same locality.

Of the four, *Kallstroemia perennans* has the most restricted distribution *(Map 15)*. This rare perennial of the Chihuahuan Desert is known only from Brewster, Presidio, and Val Verde counties in southwestern Texas. It appears to be the only species of the genus to be confined to a single type of substratum, having been collected only on limestone soils. Rainfall occurs mainly from June to September in the Chihuahuan Desert (Shreve, 1942), and *K. perennans* is known to flower in May, June, and September. It is found at elevations from about 650 to 1000 meters.

The most common *Kallstroemia* in the North American deserts is *K. grandiflora (Map 14)*, which is found throughout the Sonoran and Chihuahuan deserts except in Baja California, Mexico. It occurs also in the mesquite-grassland formation[1] between these two warm deserts, as do *K. californica* and *K. hirsutissima*. *Kallstroemia grandiflora* ranges south of the desert proper along the west coast of Mexico from southern Sonora to the valley of the Río Balsas and in northern Guerrero as well. In its southern extension, this species is found in thorn forest and tropical deciduous forest from southern Sonora to Colima and in arid tropical scrub in Michoacán and Guerrero. This area is characterized by arid vegetation types and marked wet and dry seasons (Shelford, 1963). *Kallstroemia grandiflora* is a typical summer annual over most of its range. It flowers mainly from July through October, following the heavy summer rains that usually fall during this time in the Sonoran and Chihuahuan deserts (Shreve, 1942, 1951), and south along the semiarid west coast of Mexico (Shelford, 1963). Flowering may take place sporadically at other times if conditions are adequate for seed germination and plant growth. Further south, from Jalisco to Guerrero, the scanty information available indicates that growth and flowering takes place sporadically from August to March, presumably following fall and winter rains, although Shelford (1963) states that most of the precipitation in this area falls from June to September. The species occurs from sea level to about 2000 meters and is found mainly on sandy soils, being particularly common on the sandy expanses of the Sonoran Desert. A number of specimens from the easternmost part of its range in Texas and Mexico have been collected on limestone and gypsum soils.

[1] Except where noted, the terms used for Mexican vegetation types are those of Leopold (1950).

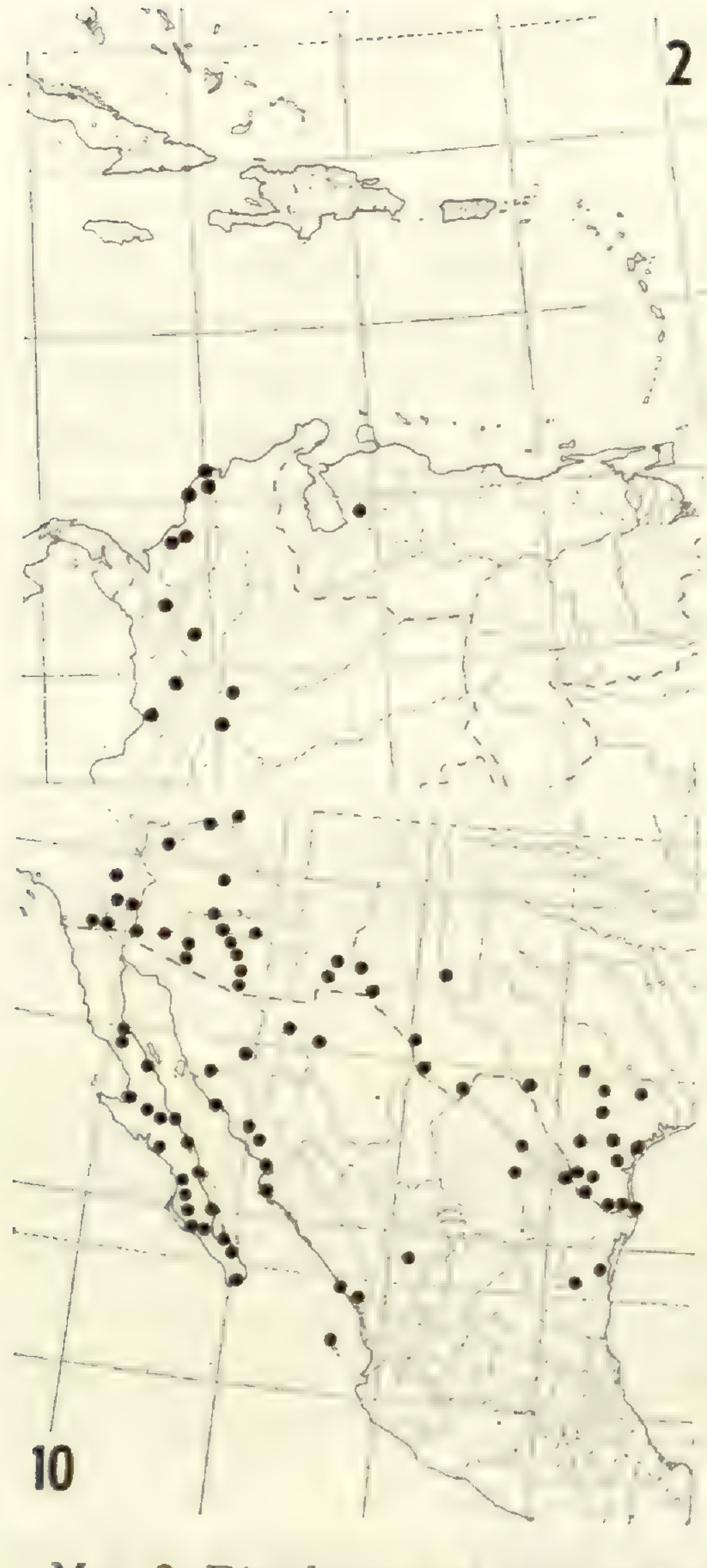
Kallstroemia californica (Map 10) is another primarily warm desert species. It occurs over much of the same area as *K. grandiflora,* but is distributed more widely in all directions except toward the south. Like that species, it continues in the thorn forest southward along the Mexican west coast. However, it extends only as far south as southern Sinaloa. Unlike *K. grandiflora, K. californica* is found in the westernmost extension of the Sonoran Desert in Baja California, where it also ranges southward into the tropical deciduous forest of the Cape Region. It occurs in the Mojave Desert of California as well, where, similar to *K. grandiflora* in the Sonoran and Chihuahuan deserts, it "may carpet the desert for miles after a rainy summer" (Munz, 1962, p. 97). *Kallstroemia californica* is found eastward through the mesquite-grassland formation and across the northern sections of the Chihuahuan Desert, where its distribution is rather spotty, to southern Texas and northeastern Mexico. In the northern area of its distribution and east of the desert, this species becomes more abundant in the various arid grassland formations it inhabits. It is common within the mesquite-grassland of southern Texas, and occurs less frequently in the *Acacia*-grassland (*fide* Shelford, 1963) both in Texas and the south and southwest in the Mexican states of Coahuila, Nuevo León and Tamaulipas. Throughout most of its range, *K. californica* grows and flowers from July through October, following the summer rains. Exceptions are in Texas, where flowering may begin in May or occasionally as early as March, and in Baja California. In the latter area, the plants behave as winter annuals, growing and flowering from August through March, following fall and winter rains. Such a growth cycle is unusual for the genus, but it is not particularly so for the area, as the Sonoran Desert in Baja California is extremely poor in summer annuals (Shreve, 1951). Like *K. grandiflora, K. californica* is to be found mainly in sandy disturbed areas, where it occurs mainly at lower elevations, but extends from sea level to about 1600 meters. This species apparently has increased its range eastward in recent times, concomitant with the invasion of the grasslands by arid scrub.

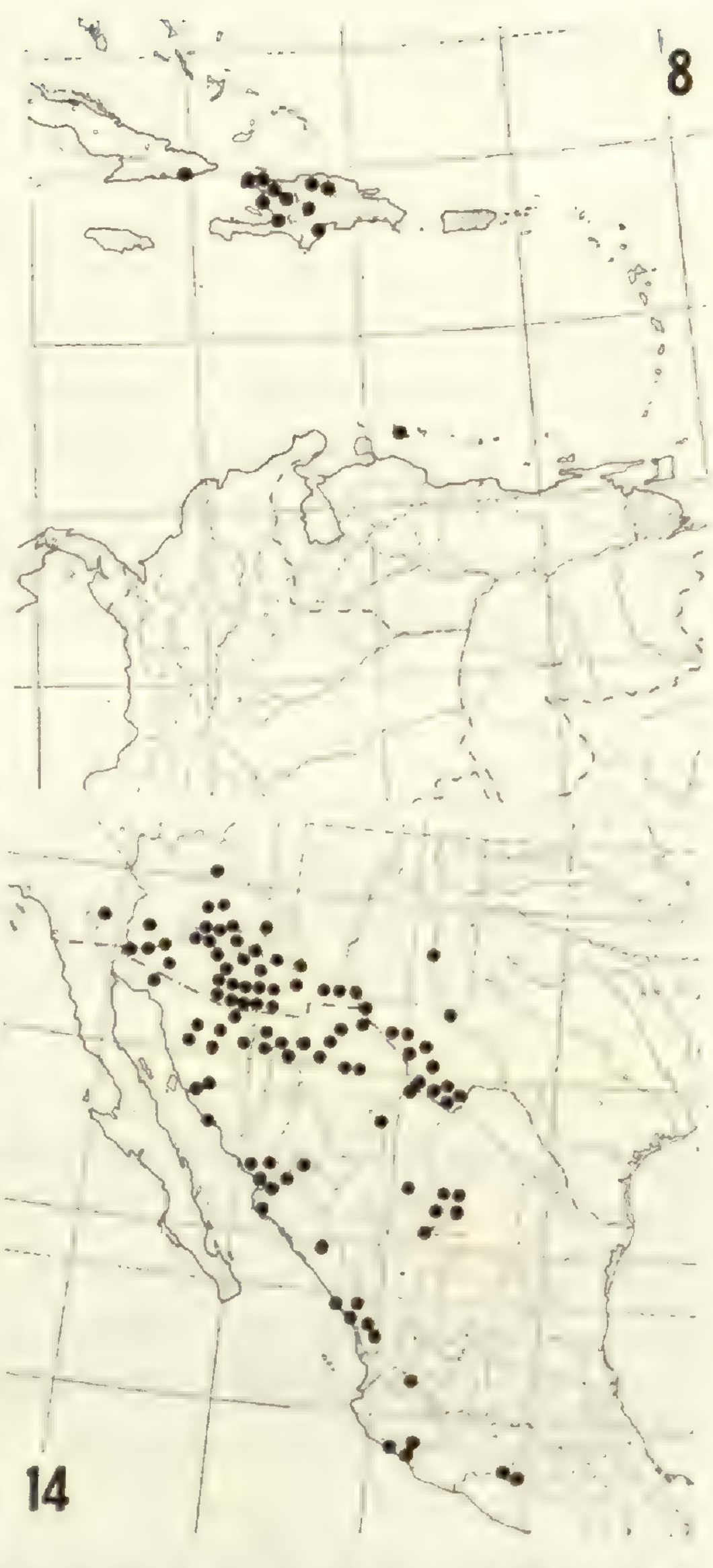
The fourth species of the warm desert group, *Kallstroemia hirsutissima (Map 7),* is distributed most commonly in the Chihuahuan Desert, but it extends northwestward through the mesquite-grassland formation to that portion of the Sonoran Desert

MAP 1. Distribution of *Kallstroemia maxima*. MAP 4. New World distribution of *Kallstroemia pubescens*, exclusive of Ecuador and Perú (see MAP 5).

in southeastern Arizona that Shreve (1951) has called the Arizona Upland. As is true of *K. californica*, *K. hirsutissima* occurs to the east in the mesquite-grassland and *Acacia*-grassland formations of southern Texas and northeastern Mexico. However, it has not been collected often in the latter area. It is a summer annual, known to germinate, grow, and flower only from June to October, but mostly from July through September. *Kallstroemia hirsutissima* is found from sea level to about 1700 meters, mainly at higher elevations. Perhaps, as is suggested for *K. californica*, it has recently spread eastward into the semiarid grasslands.

There is a fifth species which ranges to some extent into the North American warm deserts, but in contrast to the others, it appears to be the only *Kallstroemia* that is indigenous to areas characterized by various grassland formations. *Kallstroemia parviflora (Maps 5, 16)* has been collected from Illinois south to the central Mexican states of Guanajuato, Querétaro, and Hidalgo. It occurs from California east to Mississippi and has been introduced into Peru as well. In Mexico, *K. parviflora* is almost entirely confined to the mesquite-grassland, but it has been collected sporadically in the Chihuahuan Desert also. To the northwest, it has been found occasionally in the United States in the Sonoran and Mojave deserts and beyond. The species is most common in Texas, from whence it ranges northward through New Mexico and Oklahoma to Colorado and Kansas, mainly occurring west of 96° longitude. *Kallstroemia parviflora* occurs sporadically to the east into Missouri and Illinois, where it has been introduced along the railroads, and it is also known from a single collection in Mississippi. In the United States this species is to be found mainly in the mesquite-grassland, and the different grasslands characterized by short-grass, mixed-grass, and tall-grass (*fide* Shelford, 1963). It occurs sporadically outside of these areas. Flowering is mainly from July to September throughout this vast range. Germination and growth follow the summer rains, which decrease in amplitude toward the north. However, growth and flowering may take place at other times as well if conditions of moisture and temperature are adequate. It is interesting to note that this species remains a summer annual where it has been introduced in Peru, flowering from November through April. There it has been collected in localities characterized by different communities of subtropical scrub receiving summer rainfall (Tosi,





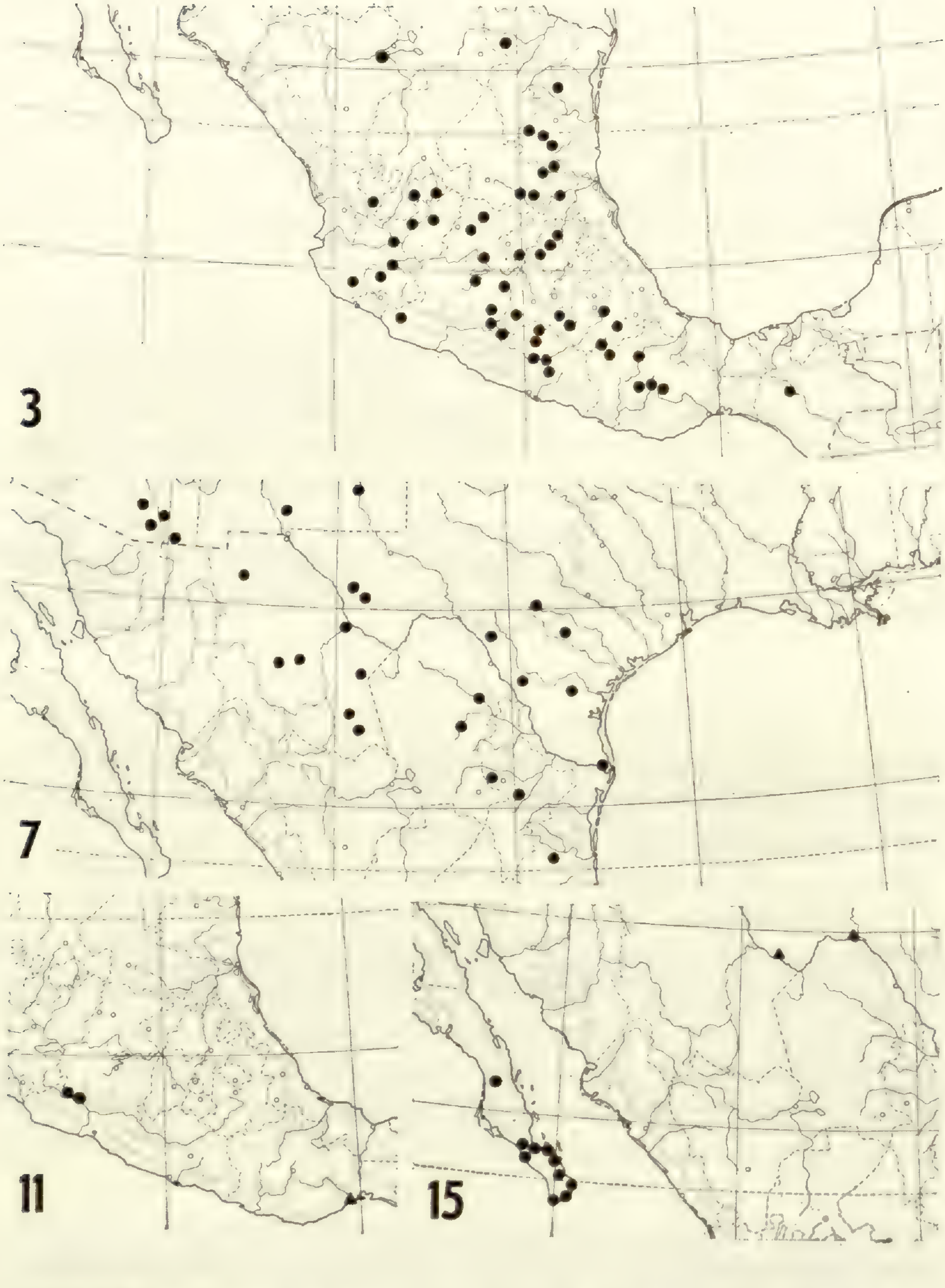
Map 2. Distribution of *Kallstroemia maxima* × *K. pubescens*?. Map 8. Distribution of *Kallstroemia curta*. Map 10. Distribution of *Kallstroemia californica*. Map 14. Distribution of *Kallstroemia grandiflora*.

1960). *Kallstroemia parviflora* is to be found usually in sandy disturbed areas, but in a report on the desert gypsum flora of western Texas and adjacent New Mexico, Waterfall (1946) indicated that this species (reported as *K. brachystylis*) grew well on gypsum. However, he thought that the plants observed were probably gypsum tolerant, rather than gypsophilous.

There are six species of *Kallstroemia* that occur in Mexico in addition to three of the four species discussed above. Of the six, four are endemic to Mexico, and three of these endemics have a restricted distribution. *Kallstroemia standleyi* appears to have the narrowest distribution of the Mexican endemics, but further investigation will undoubtedly prove it to have a wider range than is known at present. *Kallstroemia standleyi* has been collected only at the type locality, on sand dunes near the beach, one-half mile east of Salina Cruz, Oaxaca *(Map 11)*. Leopold (1950) and Shelford (1963) characterize the vegetation of this general area as savannah, but from personal observation I would say that the coastal area in the immediate vicinity of Salina Cruz is better termed arid tropical scrub. It is possible that the presence there of a xerophytic vegetation type may be a secondary phenomenon due to man's interference through cutting and grazing. This species is known to flower in July.

The second Mexican endemic with a restricted distribution is *Kallstroemia hintonii*, known only from elevations of from 300 to 400 meters in the general region of Apatzingán, Michoacán *(Map 11)*. Although *K. hintonii* has been collected only a half-dozen times, it does not appear to be rare where it is found. Leavenworth (1940) states that it may be seen "coloring whole fields at times," and I have found a population which stretched for about two miles along both sides of the road between Apatzingán and Aguililla, Michoacán. The vegetation of the Apatzingán area is tropical deciduous forest and arid tropical scrub. Summer rains predominate and occur from June to September (Shelford, 1963). *Kallstroemia hintonii* is known to flower in August, September, and December.

The southern part of the Mexican territory of Baja California Sur contains the endemic *Kallstroemia peninsularis (Map 15)*. This species is found mainly in low sandy areas and sandy beaches in the tropical deciduous forest of the Cape Region, but it also occurs occasionally to the west and north in the Sonoran Desert.



Map 3. Distribution of *Kallstroemia rosei*. Map 7. Distribution of *Kallstroemia hirsutissima*. Map 11. Distribution of *Kallstroemia standleyi* (triangle) and *K. hintonii*. Map 15. Distribution of *Kallstroemia peninsularis* and *K. perennans* (triangles).

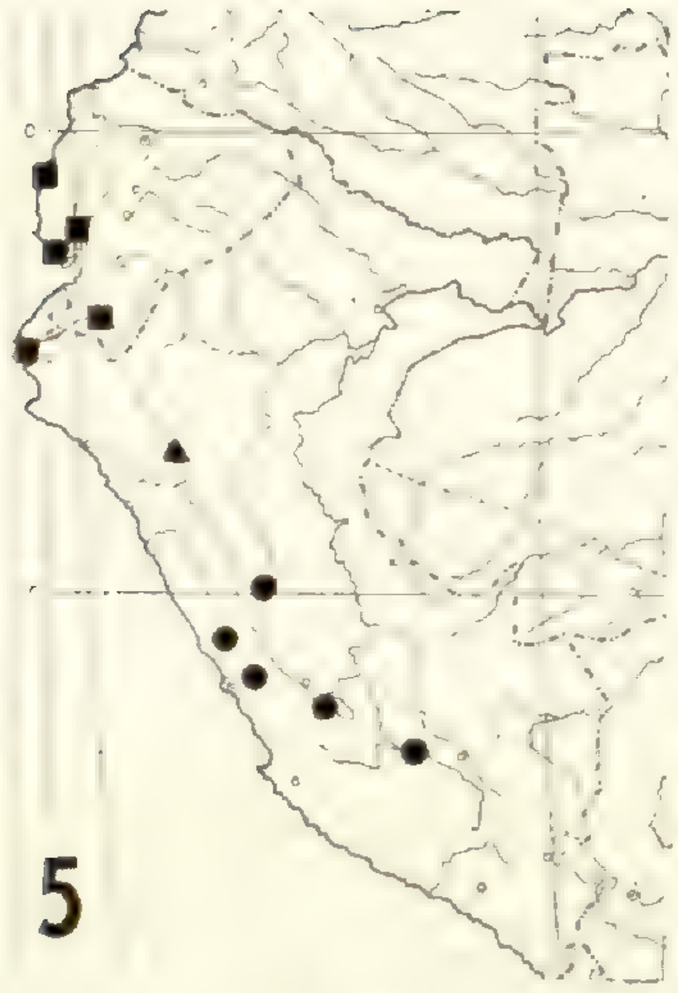
The Cape Region of Baja California differs from the adjacent desert area in that the more copious rains usually fall during the summer months, although winter rains are not unknown (Shreve, 1937). *Kallstroemia peninsularis* is known to flower from August through March, following both summer and winter rains.

The most widespread *Kallstroemia* endemic of Mexico is also the one found in the most mesophytic vegetation type. *Kallstroemia rosei (Map 3)* appears originally to have been restricted to open disturbed sites in the pine-oak forest of central and northeastern Mexico, but man has distributed it into lower and more xerophytic habitats, especially Guerrero and Michoacán. At present, it occurs from 200 to 3150 meters, mainly at higher elevations. *Kallstroemia rosei* ranges from the Sierra Madre Oriental in Nuevo León to the Sierra de Oaxaca and Sierra Madre del Sur in central Oaxaca, and from Jalisco to Puebla in the mountains of central Mexico. It is very common also in the Río Balsas basin and is found sporadically at lower elevations elsewhere. The pine-oak forest area of Mexico has a rainy season that generally extends from June through September (Shelford, 1963), and *K. rosei* usually flowers during this time, although scattered instances of flowering until March are known.

The Caribbean region has three species of *Kallstroemia*, two of which have a very wide distribution, both occurring outside of this area. In contrast to their more temperate congeners, these more tropical species may be found flowering thoughout the year. Seed germination and growth appear to be almost wholly dependent upon the presence of adequate moisture—at least this appears to be true in their native habitats.

The island of Hispaniola seems to be the original area occupied by *Kallstroemia curta*. It has probably been introduced into Cuba and the Netherlands Antilles islands of Aruba, Bonaire, and Curaçao *(Map 8)*. This species is the most restricted of the Caribbean members of the genus. It occurs from sea level to 1300 meters but is found mainly at lower elevations.

One of the most widespread species of *Kallstroemia* is *K. maxima (Map 1)*. It is commonest in the islands of the Caribbean and in western Central America. This species also ranges across northern South America and northward along both coasts of Mexico to the Tropic of Cancer and beyond. In the southeastern United States it occurs as far north as South Carolina, and it has



Map 5. Distribution of *Kallstroemia pubescens* (squares) in Ecuador and Peru, *K. pennellii* (triangle) and *K. parviflora* in South America. Map 6. Distribution of *Kallstroemia tucumanensis*. Map 12. Distribution of *Kallstroemia boliviana*. Map 13. Distribution of *Kallstroemia tribuloides*.

been introduced into Brenham County, Texas, where it persists. This weedy species of sandy disturbed soils has been collected at elevations ranging from sea level to about 1350 meters, but it is especially prevalent along roadsides and in cultivated areas at lower elevations. *Kallstroemia maxima* rarely is to be found outside of areas that are frost-free the year around.

A species that occurs sympatrically with *Kallstroemia maxima* over much of its range is *K. pubescens (Maps 4, 5)*. Although the two are found growing in the same locality occasionally, they appear to be at least partially isolated ecologically. *Kallstroemia pubescens* tends to be found in sandier situations at slightly higher elevations than *K. maxima*. It occurs from sea level to 1400 meters, being most common at lower elevations. It is commoner than *K. maxima* in the Lesser Antilles and is almost completely absent from the Greater Antilles. *Kallstroemia pubescens* is found in disturbed areas through western Central America as far north as Yucatán on the southeastern coast of Mexico, while on the west coast it reaches southern Sinaloa. It is less common through this area than *K. maxima*. However, *K. pubescens* ranges further south than the latter species, occurring in the xerophytic coastal area (*fide* Svenson, 1946a) of Ecuador and northern Peru. It is also known from a single locality in western Florida. This species flowers the year around, except in Ecuador and Peru, where it flowers during the rainy season from February to April. It is the only *Kallstroemia* known outside of the New World, having been introduced to coastal Ghana and Nigeria (Keay, 1955) and West Bengal, India (Bennet, 1965).

Five species of *Kallstroemia* are endemic to South America. Of these, two have been found growing in the same localities, and mixed collections of herbarium specimens are sometimes found. These two species, *K. tribuloides* and *K. tucumanensis*, have the southernmost distributions in the genus *(Maps 6, 13)*. Both of them are native to a region characterized by xerophilous scrublands (Cárdenas, 1945; Cabrera, 1951) which stretch along the eastern base of the Andes from southern Bolivia to central Argentina. They have been collected at elevations from 300 to 1800 meters in this area. This arid and semiarid region is similar to those of North America where the genus is found, and summer rain predominates (Cabrera, 1951). Seed germination and plant growth take place following these rains. *Kallstroemia tucuman-*

MAP 9. Distribution of *Kallstroemia adscendens*. MAP 16. Distribution of *Kallstroemia parviflora* in North America (see MAP 5 for South American distribution).

ensis flowers from November to April, and *K. tribuloides* from November to May. The former has been found farther north and south than *K. tribuloides*, but the latter also is known from northeastern Brazil *(Map 13)* in an area dominated by deciduous scrub forest (Smith & Johnston, 1945). *Kallstroemia tribuloides* is thought to have been introduced to Brazil from Argentina (Descole, *et al.*, 1939). The Brazilian collections that I have seen were mainly from sandy places along the Rio São Francisco, the largest river in the area. This species is also found in similar situations in Argentina.

Another species which occurs in Bolivia is *Kallstroemia boliviana*. It is found in the semiarid valleys of the eastern slopes of the Cordillera Oriental at elevations from about 1100 to 2800 meters *(Map 12)*. A single Peruvian collection is known from a comparable area at an elevation of 1300 to 1400 meters where the vegetation is subtropical spiny shrubland (Tosi, 1960). *Kallstroemia boliviana* flowers from October through April. The interandean region of Bolivia, where it is to be found generally, receives summer precipitation from November through April (Franze, 1927).

The Peruvian *Kallstroemia pennellii* is known only from the type locality along the Río Marañon above Balsas, Cajamarca, at an altitude between 700 and 900 meters *(Map 5)*. The vegetation of this area is tropical spiny forest (Tosi, 1960), a hot semiarid formation of northern Peru. This locality is characterized by summer rains and very high temperatures. The single collection known flowered in April.

The fifth, wholly South American *Kallstroemia*, is *K. adscendens*, an endemic of the Galápagos Islands, Ecuador *(Map 9)*. It is known from the islands of Charles, Chatham, Duncan, Gardner, and Hood. It has been collected on beaches and lower slopes of the arid coastal zone, where the vegetation is predominantly xerophytic shrubs and subshrubs (Robinson, 1902). According to Svenson (1946a), sporadic rains occur in the islands from February to June. Flowering of *K. adscendens* is known to take place from April through June.

Based on a broad scope of information, a certain correlation may be seen between the occurrence of *Kallstroemia* and regions with high summer temperatures and summer precipitation, although the genus is by no means restricted to such areas. Those

tropical species occurring in regions where rainfall and high temperatures may be found throughout the year grow and flower at any time. However, where the tropical representatives of the genus are encountered in areas with definite wet and dry seasons, they show the same periodicity in seed germination and plant growth as the temperate species found under similar circumstances.

Habitat

Species of *Kallstroemia* are invariably found in open, disturbed habitats. These habitats may be natural, as in desert areas, or artificial, such as those provided by man in his rapid destruction of the natural vegetation. Plants of open natural habitats in deserts and sparsely occupied sand dunes, beaches, etc., have the greatest facility for spreading into and colonizing artificially created habitats (Salisbury, 1942, 1961). Open desert land, sand dunes, and beaches were undoubtedly the prime habitats of *Kallstroemia* prior to the invasion of the New World by European man. Since then, and perhaps to a limited extent even before, the resulting deterioration of the natural vegetative cover and the concomitant increase of disturbed habitats have provided numerous new areas into which species of *Kallstroemia* could migrate. At present, the most common situations where species of the genus are to be found as weeds are roadsides and cultivated areas. Clements (1920) has stated that the presence of *K. californica* (listed as *K. brachystylis*), *K. grandiflora*, *K. hirsutissima*, and *K. parviflora* is an indication of overgrazing in the arid grasslands of the southwestern United States. *Kallstroemia parviflora* became a troublesome weed in southern Kansas soon after the beginning of cultivation in that area (Carleton, 1892; Holzinger, 1892).

Dispersal Mechanisms

Species of the genus inhabiting desert areas probably are dispersed through the action of rain wash. However, sea water dispersal probably does not take place in *Kallstroemia*. I have observed that the mericarps of two Caribbean species, *K. maxima* and *K. pubescens*, like those of *Tribulus cistoides* (Guppy, 1906), will not float in sea water. Unlike most of *Tribulus*, the mericarps of *Kallstroemia* lack appendages that would allow them to cling

to the outer surface of an animal, with the exception of those with rough tubercles as in *K. californica* and *K. standleyi,* and those with hispid trichomes as in *K. perennans.* However, animal dispersal may take place because of the mucilaginous sheath secreted by the mericarps when they are wet. This sheath could allow them to adhere to an animal and in drying bind them temporarily to skin, fur, or feathers. Mucilage produced by the wetted mericarps may not only increase chances of dispersal, but it could act to anchor the mericarps to the soil, providing a decided advantage for the small disseminules of species growing in open situations. Dispersal of disseminules through formation of an adherent mucilage is well documented (e.g., Salisbury, 1961).

The hard pericarp of the mericarps also may allow them to be eaten and passed through the digestive tract of an animal unharmed. This ingestion could act to break seed dormancy as well. There is no concrete evidence for internal transport by animals, but it is known that in Arizona *Kallstroemia grandiflora* seeds are fed upon by quail (Griner, 1940) and the herbage is eaten by herbivores (McGinnies, 1922). In Peru, *K. parviflora* is browsed by livestock (Macbride, 1949). Similarly, *K. tribuloides* and *K. tucumanensis* are browsed in Argentina (Ruíz Leal, 1947, 1951).

Today the animal most important in dispersal of the genus is man. The southward spread of *Kallstroemia tucumanensis* has been facilitated through man's action, probably by the mericarps being imbedded in mud attached to vehicles (Ruíz Leal, 1951). Undoubtedly, man has been instrumental in carrying *K. maxima* to Texas, *K. parviflora* to Peru, and *K. pubescens* to West Africa and India. In the latter case, *K. pubescens* was discovered along a railroad right-of-way (Bennet, 1965). Railroads appear to have played a leading role in the spread of *K. parviflora* north and east from its presumed original area of occupation in North America. Early collections show this species to have advanced mainly along railroad rights-of-way. But now, like most other species in the genus, it is primarily dispersed by the automobile. This is so often the case that species of *Kallstroemia* are frequently to be found in disturbed areas along roads and highways.

Vegetative dispersal probably does not take place. There is no evidence for vegetative reproduction in the genus. This is not unexpected in a group of plants that mostly are ephemeral annuals.

Distribution and Self-compatibility

The prevelance of self-compatibility in desert annuals and particularly in weedy plants is well documented (cf., Stebbins, 1950; Baker, 1955; Salisbury, 1961). From observations on the reproductive biology of *Kallstroemia*, it can be inferred that all species of the genus, with the probable exception of *K. perennans*, are self-compatible. There are three situations under which self-compatibility proves to be advantageous in the survival and spread of a species: (1) Individuals may resort to self-pollination if conditions are unfavorable for outcrossing, as in the absence of pollinators (Stebbins, 1950)—this situation also could arise where individuals are so widely spaced that the frequency of outcrossing is restricted (Fryxell, 1957); (2) In cases of long distance dispersal, only a single disseminule is necessary for the establishment of a new colony if the species is self-compatible (Baker, 1955); (3) In the colonization of temporary habitats, such as those inhabited by weeds, there is a premium placed on species that can rapidly build up populations of individuals that are as well adapted as their parents to these temporary situations (Stebbins, 1950). This can be accomplished most successfully by relatively homozygous individuals belonging to self-fertilizing lines (Stebbins, 1957).

The above processes undoubtedly have occurred in the past and are presently ocurring in *Kallstroemia*. Absence of pollinators and wide separation of individuals (i.e., as weeds along roadsides) are surmounted through selfing. Isolated individuals invariably set seed in the field. The presence of self-compatibility has probably been a factor in the introduction and persistence of *K. maxima* in Texas, *K. parviflora* in Peru, *K. pubescens* in West Africa and India, and *K. tribuloides* in northeastern Brazil. In addition, it has aided in the rapid spread of most species to disturbed environments. Direct evidence for rapid build-up through preadaptation is lacking because nothing is known concerning the genetics of the genus.

Self-compatibility permits self-fertilization, but it does not insure it. This insurance is provided in *Kallstroemia* by the stamen and petal movements which act to appress pollen to the receptive stigma. However, self-fertilization is facultative, and outcrossing probably predominates under many circumstances. Stamen and petal movement occur whether outcrossing has taken place or not.

It would be interesting to know whether there is any differential pollen tube growth between selfed and crossed pollen.

Biotic Relationships

Occasional individuals of *Kallstroemia hirsutissima, K. maxima, K. parviflora,* and *K. tucumanensis* have been encountered in which the nodes or fruits had been attacked by insect larvae. Some Central American populations of *K. maxima* examined in the field were highly infested with these larvae to the extent that practically every fruit had been attacked. A small black aphid is commonly found on the herbage of many species of *Kallstroemia.* North American specimens of the introduced *Tribulus terrestris* commonly are covered with a similar aphid.

Two insects that have been introduced into the western United States for the biological control of *Tribulus terrestris* may prove harmful to indigenous species of *Kallstroemia,* and perhaps to *Larrea tridentata,* also. It has been reported by Andres and Angalet (1963) that adults of these insects will feed on the leaves and stems of *Kallstroemia californica, K. grandiflora, Larrea tridentata,* and *Zygophyllum fabago* (an introduced weed in California), as well as *Tribulus terrestris. Microlarinus lareynii* (Jacquelin du Val), a seed weevil, will oviposit on fruits of both *K. californica* and *K. grandiflora,* but larvae develop to maturity only in the latter. *Microlarinus lypriformis* (Wollaston), a stem weevil, will not oviposit on *Kallstroemia.*

A discussion of insect pollen vectors of *Kallstroemia* is found above in the section on reproductive biology.

At least two species of *Kallstroemia* are parasitized by other plants. I have seen specimens of *K. grandiflora* from Arizona and Sonora, Mexico, and *K. maxima* from Puerto Rico and Yucatán, Mexico, that were host to *Cuscuta umbellata* HBK. *Tribulus terrestris* is commonly parasitized by this species, also. Yuncker (1965) reports *C. erosa* Yunck., a species of southern Arizona and northern Mexico, on an unidentified species of *Kallstroemia.*

MORPHOLOGICAL CHARACTERS AND TAXONOMIC CRITERIA

The only previous work of a revisional nature on the genus is that of Rydberg (in Vail & Rydberg, 1910). In this and subse-

quent publications, the main criteria used in species delimitation were flower size, sepal shape, type and distribution of ovary and fruit pubescence, shape and length of the persistent style, and amount and type of pubescence on the herbage. These characters were not consistently given the same importance in every case. In the present study, it has been found that such additional characters as spatial relationship of the persistent sepals to the mature fruit, mericarp morphology, stigma shape, and leaf shape are important also. The criteria utilized by Rydberg were found in the main to be useful, albeit not always in the same context that he had used them. The fallacies of relying on single characters or those of a purely vegetative nature in classification have been clearly indicated (Rollins, 1952, 1957). Accordingly, the species are delimited herein by constellations of character combinations (*fide* Rollins, 1957). As may be seen in the following discussion, these character combinations provide the basis for a certain number of inferences concerning natural relationships in the genus.

There is a great deal of variation in the absolute size of the vegetative structures in plants of *Kallstroemia*. Size and the amount of pubescence on these parts appear to depend mainly upon the conditions under which the plants have developed. A high degree of variation in the vegetative parts is encountered frequently in plants of arid and semiarid regions. This in turn can be attributed to concomitant variation in climatic and edaphic conditions (e.g., Schweickerdt, 1937). There is also a certain amount of variation in flower and fruit size in species of *Kallstroemia* that appears to be somewhat influenced by conditions during the growth of the plant. Robust individuals have longer internodes, stems, and peduncles, and larger leaves, leaflets, flowers, and fruits, in comparison with depauperate individuals which grew under conditions of inadequate moisture, excessive disturbance, or highly alkaline soils. The latter are much smaller in all aspects, both vegetative and floral. However, the quantitative differences traceable to the influences of local environmental factors do not transcend the qualitative differences that serve to distinguish the species.

Vegetative Characters

Stems. The stems of most species of *Kallstroemia* are prostrate to decumbent in mature individuals. Exceptions are the ascending

stems of occasional plants of *K. grandiflora* and *K. parviflora* and most individuals of *K. perennans*. In *K. curta* and *K. hirsutissima* the stems are prostrate only. The taxonomic value of the stem habit itself is limited, but it can be utilized in concert with other morphological traits. Lengths of the stems and internodes at times have been used to help delimit species, but these characters, like most others of a quantitative nature, may be very variable within a species. Presence, absence, or amount of stem striation are frequently given in taxonomic descriptions for each species, but striate stems are found throughout the genus. Striations are due to a ring of cortical fibers and are not seen in the somewhat succulent stems of living plants. They become evident only after the stem has dried and shrunk.

The most useful taxonomic character of the stems is found in their pubescence. The trichomes are antrorse (directed apically) in all species but *Kallstroemia peninsularis* and a few specimens of *K. pubescens* from Peru, where they are retrorse. In most species, the stems are hirsute and sericeous, but exceptions are to be found in *K. californica* (hirsute and strigose), *K. peninsularis* (hirsute and hirtellous), *K. perennans* (hispid and strigose), *K. pennellii* (strigose), and *K. tribuloides* (sericeous). The same type pubescence as that of the stem is to be found on stipules, peduncles, petioles, and rachises.

Stipules. There is little difference in the stipules from species to species. Whether they are persistent or deciduous in mature individuals has been used in some taxonomic descriptions, but the stipules are absent only if they have been lost in the process of collecting, drying, and mounting the herbarium specimens.

Leaves. There are two distinct shapes of leaves in the genus. In one type, the terminal pair of leaflets is the largest, consequently the leaf shape is obovate. This leaf type is found in *Kallstroemia boliviana* (Fig. 10b), *K. curta* (Fig. 6b), *K. hirsutissima* (Fig. 5b), *K. maxima* (Fig. 1b), *K. pubescens* (Fig. 3b), *K. rosei* (Fig. 2b), and *K. tucumanensis* (Fig. 4b). In the second type, one of the lower pairs of leaflets is the largest, and leaf shape is elliptical. This type is found in *K. adscendens* (Fig. 7b), *K. californica* (Fig. 8b), *K. grandiflora* (Fig. 13b), *K. hintonii* (Fig. 17b), *K. parviflora* (Fig. 16b), *K. peninsularis* (Fig. 14b), *K. pennellii* (Fig. 12b), *K. perennans* (Fig. 15b), *K. standleyi* (Fig. 9b), and *K. tribuloides* (Fig. 11b). The species with obovate leaves have fewer leaflets, on the average, than the species with elliptical

leaves. This difference in leaf shape does not indicate the presence of two basic groups of related species in the genus, however. Several closely related species of *Kallstroemia* differ in leaf shape, and *K. californica* usually has elliptical leaves, but individuals occasionally are partially or wholly obovate-leaved.

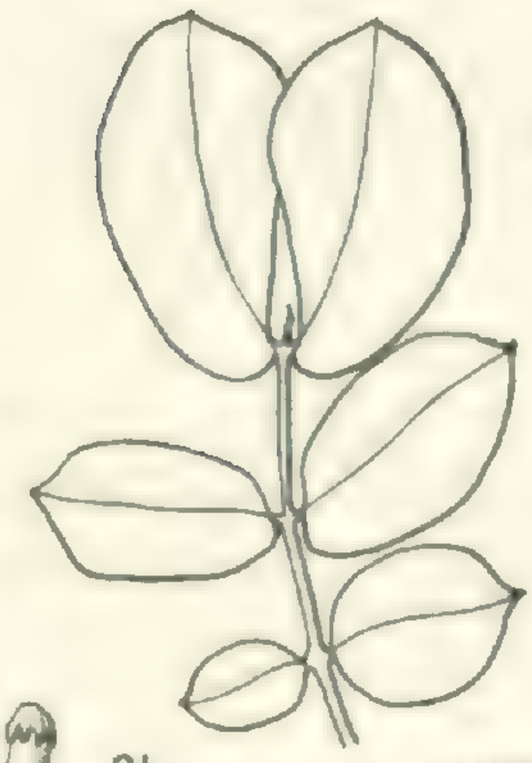
Leaf size may vary more within some species following changed environmental conditions than it does between the species. Also, there is no correlation between flower size and leaf shape or leaflet number. Leaflet number differs somewhat from species to species, but in several instances (i.e., *Kallstroemia californica, K. grandiflora, K. maxima, K. parviflora,* and *K. tribuloides)* there may be a sizeable difference in number from individual to individual within a species. Leaflet number in depauperate specimens is lower than usual. There is insufficient difference in leaf or leaflet size from species to species for either to play a major role in the discrimination of taxa within the genus.

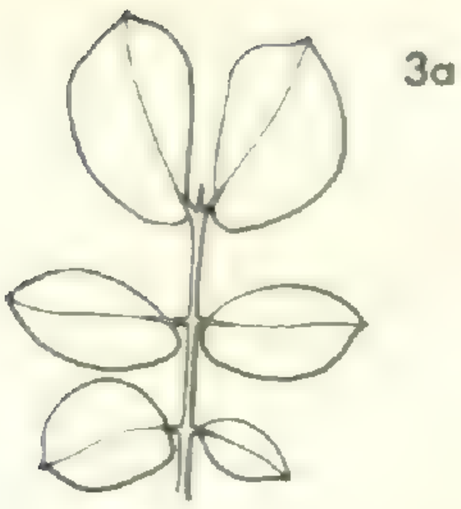
Leaflet pubescence in most species is appressed-hirsute on both surfaces of the blade. The abaxial surface is usually more pubescent than the adaxial surface. The main vein and margins are usually sericeous. Exceptions are *Kallstroemia boliviana, K. pennellii,* and *K. standleyi,* in which the pubescence of the leaflets is entirely sericeous, and *K. hintonii,* where it is wholly appressed-hirsute.

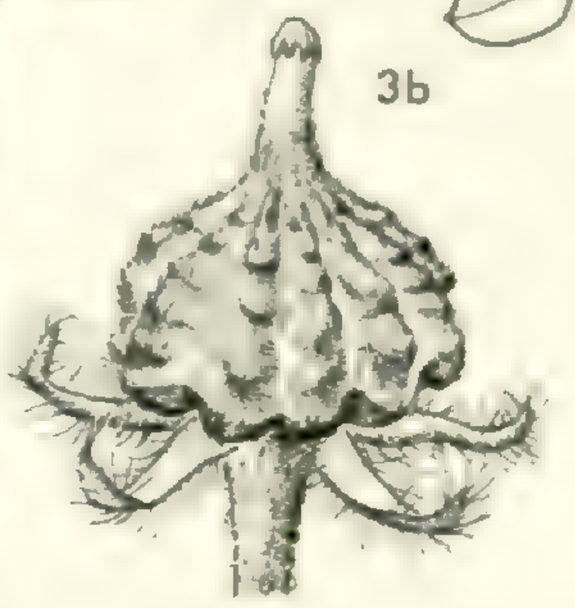
Floral Characters

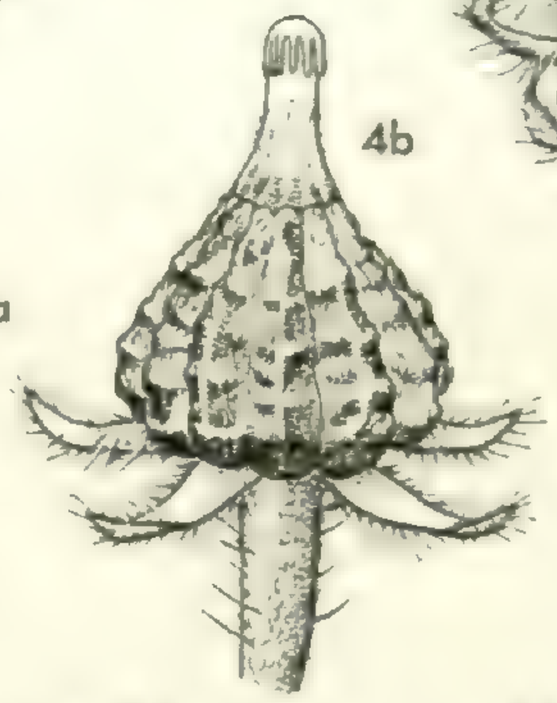
Flowers. There are substantial differences in flower size and color between different species of the genus. Flower size and color are relatively stable characters in some species, while in other species they may be quite variable. Depending upon the situation, they may be of more or less diagnostic value. There are certain correlations between flower color and size in that those species with small flowers, less than one centimeter in diameter *(Kallstroemia adscendens, K. californica, K. curta,* and *K. hirsutissima)* always have yellow petals. But petal color in the larger-flowered species varies from white through yellow to bright orange with the basal portion varying from green to red. In these latter species the petal base is usually somewhat darker than the distal portion. In some populations of *K. grandiflora, K. hintonii,* and *K. maxima* the base is a bright red.

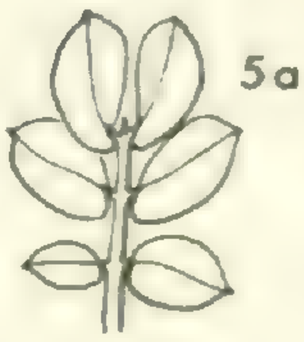
Calyx. Following anthesis, there are three basic configurations

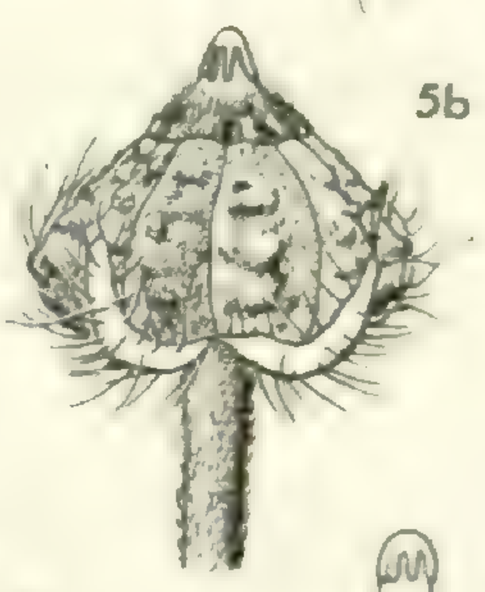












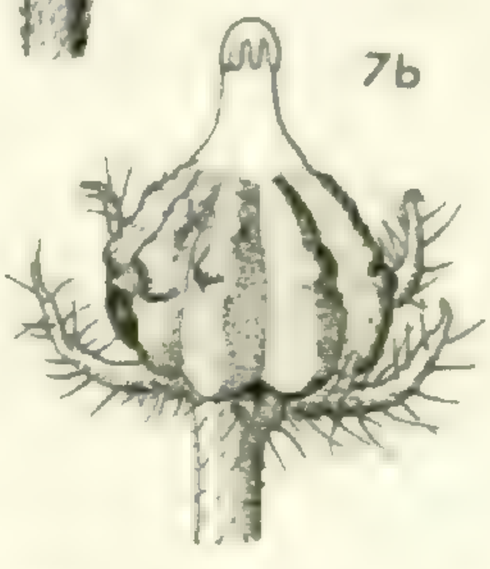


FIG. 1. *Kallstroemia maxima: a,* leaf, *b,* fruit, of *Porter 1035.* FIG. 2. *Kallstroemia rosei: a,* leaf, *b,* fruit, of *Porter 1375.* FIG. 3. *Kallstroemia pubescens: a,* leaf, *b,* fruit, of *Porter 1214.* FIG. 4. *Kallstroemia tucumanensis: a,* leaf, *b,* fruit, of *Pflanz 4041.* FIG. 5. *Kallstroemia hirsutissima: a,* leaf, *b,* fruit, of *Stewart 1166.* FIG. 6. *Kallstroemia curta: a,* leaf of *Leonard & Leonard 13322; b,* fruit of *Ekman 15981.* FIG. 7. *Kallstroemia adscendens: a,* leaf, *b,* fruit, of *Snodgrass & Heller 756.*

of the sepals which are very useful taxonomically. They may clasp the base of the mature fruit, with only the scarious margins folding involutely under, if at all, as in *Kallstroemia boliviana* (Fig. 10a), *K. hintonii* (Fig. 17a), *K. hirsutissima* (Fig. 5a), *K. maxima* (Fig. 1a), *K. pennellii* (Fig. 12a), and *K. tribuloides* (Fig. 11a). They may spread from the base of the mature fruit, occasionally curving upward, with the margins sharply folding involutely upon one another and making the sepals appear linear or linear-lanceolate to the naked eye, as in *K. adscendens* (Fig. 7a), *K. californica* (sepals usually deciduous; Fig. 8a), *K. curta* (Fig. 6a), *K. pubescens* (Fig. 3a), *K. rosei* (Fig. 2a), *K. standleyi* (Fig. 9a), and *K. tucumanensis* (Fig. 4a). Instead of spreading, the sepals may curve upward around the mature fruit, shriveling and turning brown, as in *K. grandiflora* (Fig. 13a), *K. parviflora* (Fig. 16a), *K. peninsularis* (Fig. 14a), or *K. perennans* (Fig. 15a).

A further character is the type of pubescence present on the sepals (see above figures). The indument may be hirsute *(Kallstroemia curta, K. hintonii, K. hirsutissima,* and *K. maxima),* hirsute and strigose *(K. adscendens, K. boliviana, K. rosei,* and *K. tribuloides),* hispid and strigose *(K. grandiflora, K. parviflora,* and *K. perennans),* hispid and hirtellous *(K. peninsularis),* hispidulous *(K. pubescens* and *K. tucumanensis),* sericeous *(K. pennellii* and *K. standleyi),* or strigose to hirsutulous and strigillose *(K. californica).* There is an evident correlation between the presence of hispid and strigose pubescence and the upwardly turned sepals which ultimately shrivel and turn brown.

Corolla. See the discussion above under flowers.

Androecium. The filaments are filiform or subulate in all species except *Kallstroemia hintonii,* where they are winged at the base. They are sufficiently long to extend the anthers upward and appress them to the stigma except in *K. perennans,* where the filaments reach only two-thirds up the length of the style. Filament color is correlated with the color of the petal base. Because the colors of the two are always the same, they are assumed to be genetically linked.

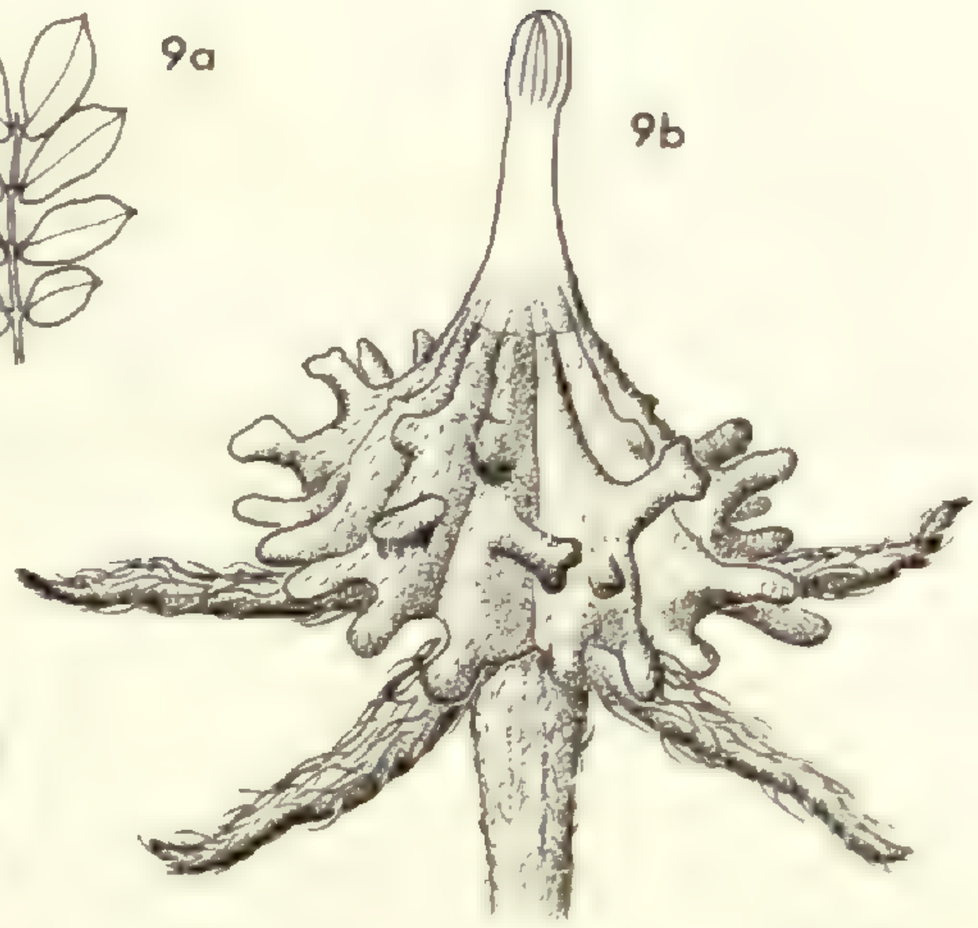
In a given flower, anther and pollen color are the same. However, the color may differ both between and within species. The color range is from yellow to red. In *Kallstroemia adscendens, K. californica, K. curta, K. hirsutissima, K. parviflora, K. peninsularis, K. standleyi,* and *K. tucumanensis* the color is yellow; in *K. boliv-*

iana, K. hintonii, K. perennans, and *K. tribuloides* it is orange or red. In the remaining species, populations of individuals may have anthers and pollen that are some shade of either yellow, orange, or red. *Kallstroemia maxima* and *K. pubescens* may be either yellow or red; *K. grandiflora* and *K. rosei* usually are orange or red, rarely yellow. The anther and pollen color of *K. pennellii* is unknown. Yellow-flowered individuals usually have yellow anthers and pollen as well, but this is not invariably the case (e.g., as in *K. hintonii*). There is a correlation and presumably genetic linkage between a red petal base and red anthers and pollen in *K. grandiflora, K. hintonii,* and *K. maxima.* These color differences usually are reliable criteria only in fresh material, because of fading and color changes which accompany the drying of specimens.

Anthers in *Kallstroemia standleyi* and *K. tribuloides* are regularly linear-oblong; otherwise they are ovoid or globose throughout the remainder of the genus. However, occasional specimens of *K. grandiflora, K. maxima, K. parviflora, K. rosei,* and *K. tribuloides* have been seen in which one whorl of stamens has linear anthers. Occasionally, one whorl of stamens has abortive anthers.

Gynoecium. The ovary is ovoid or globose in most species of *Kallstroemia,* but in *K. boliviana, K. rosei,* and *K. tribuloides* it is conical, and pyramidal in *K. pubescens.* It is almost always pubescent, being glabrous only in *K. hintonii, K. maxima,* and *K. tribuloides,* but it is occasionally strigose in *K. maxima.* As with all other floral structures, ovary size varies with overall flower size, being correspondingly large or small.

Style length, like ovary size, differs with the flower size, smaller-flowered species having shorter styles. There may be a certain amount of variation of style length within a species, but in *Kallstroemia grandiflora, K. hintonii, K. maxima, K. parviflora, K. peninsularis, K. pennellii, K. perennans, K. rosei, K. standleyi,* and *K. tribuloides* it is nearly always longer than the ovary. In the other species, it is equal to or shorter than the ovary. Style shape in the genus is mostly cylindrical above and conical below, but *K. adscendens, K. boliviana, K. californica, K. curta, K. hirsutissima, K. pubescens* (rarely cylindrical above), *K. rosei,* and *K. tucumanensis* all have more or less stout conical styles. Therefore, one can see a definite correlation between style length and



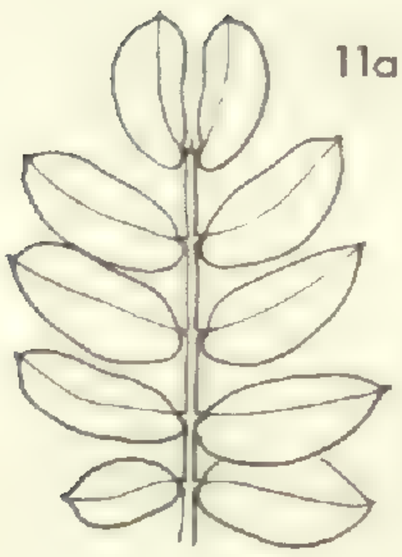


FIG. 8. *Kallstroemia californica: a,* leaf, *b,* fruit, of *M. E. Jones* 24963. FIG. 9. *Kallstroemia standleyi: a,* leaf, *b,* fruit, of *Morley* 861 (type). FIG. 10. *Kallstroemia boliviana: a,* leaf, *b,* fruit, of *Cárdenas* 3860. FIG. 11. *Kallstroemia tribuloides: a,* leaf, *b,* fruit, of *Schreiter s. n.* FIG. 12. *Kallstroemia pennellii: a,* leaf, *b,* fruit, of *Pennell 15185* (type). FIG. 13. *Kallstroemia grandiflora: a,* leaf, *b,* fruit, of *Gentry 1667.*

shape, stout, conical styles generally being shorter than the ovary. There are differences in the amount, type, and distribution of stylar pubescence. Most species are glabrous to strigose in this character, but the style is hirsute in *K. perennans*. In *K. hirsutissima* and *K. rosei* it is surrounded at the base by a ring of hirsute pubescence, a feature that is especially pronounced in the latter species.

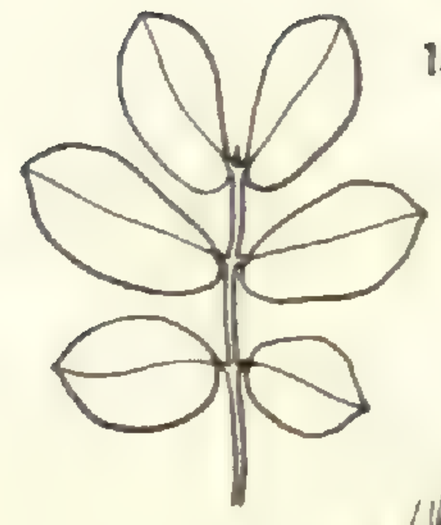
There appear to be three fundamental stigma types in *Kallstroemia*. The stigma may be capitate and obscurely ten-lobed, as in *K. maxima* (Fig. 1a), *K. pubescens* (Fig. 3a), and *K. rosei* (Fig. 2a). The stigma may be oblong and ten-ridged, as in *K. boliviana* (Fig. 10a), *K. parviflora* (Fig. 16a), *K. pennellii* (Fig. 12a), *K. perennans* (Fig. 15a), *K. standleyi* (Fig. 9a), *K. tribuloides* (Fig. 11a), or *K. tucumanensis* (Fig. 4a). It may be clavate and ten-ridged, as in *K. adscendens* (Fig. 7a), *K. californica* (Fig. 8a), *K. curta* (Fig. 6a), *K. grandiflora* (Fig. 13a), *K. hintonii* (Fig. 17a), *K. hirsutissima* (Fig. 5a), and *K. peninsularis* (Fig. 14a). There are no general correlations between stigma type and flower size or style length.

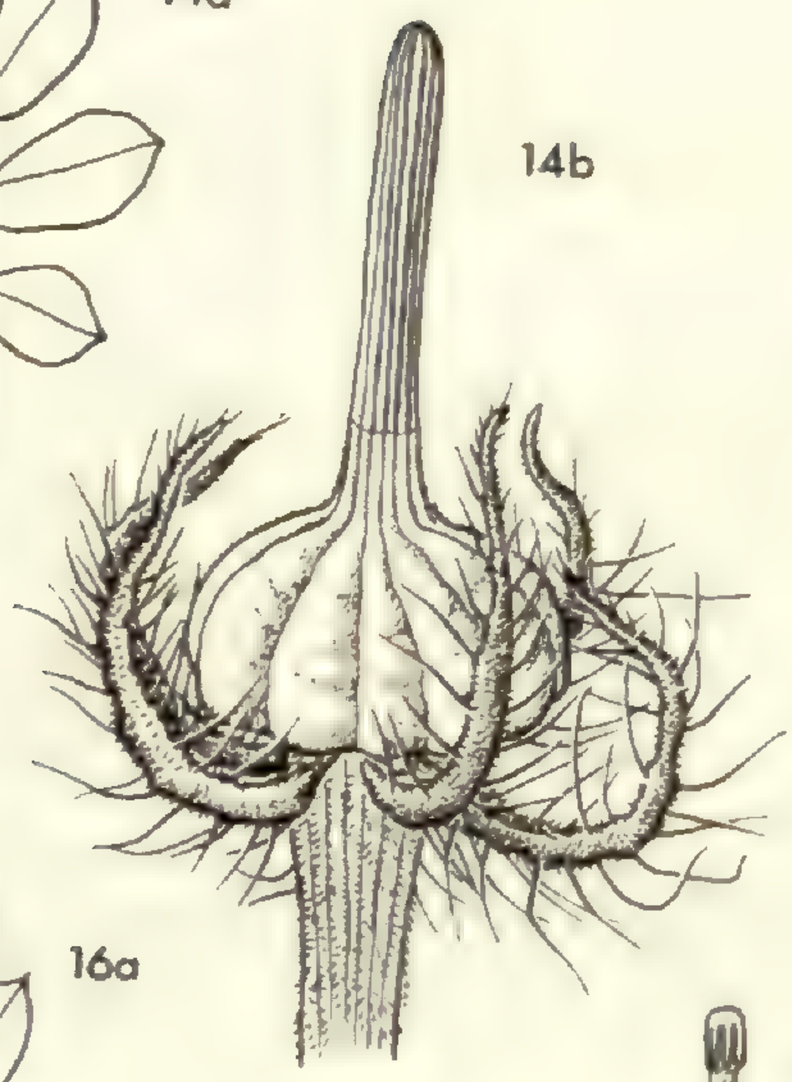
The stigmatic surface is papillose in all species but *Kallstroemia perennans*, where it is coarsely canescent (Fig. 15a). It extends downward almost to the stylar base in *K. peninsularis* (Fig. 14a) but is terminal in all other species.

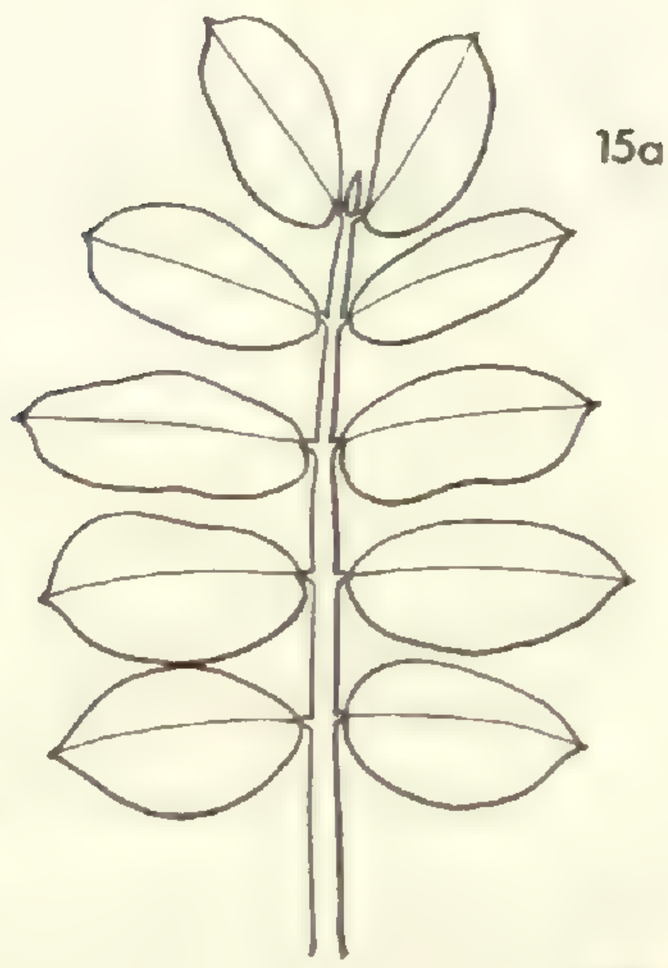
Fruit Characters

Peduncles. The length of the peduncle in fruit is of some taxonomic significance. In *Kallstroemia californica, K. curta, K. hirsutissima, K. perennans, K. pubescens, K. rosei,* and *K. tucumanensis* it is usually shorter than the subtending leaf. In all other species, with the exception of *K. peninsularis*, it is usually longer. The fruiting peduncle of *K. peninsularis* may be longer or shorter than its subtending leaf.

Shape of the peduncle in fruit differs from species to species. In *Kallstroemia boliviana, K. rosei, K. standleyi,* and *K. tribuloides* it is curved. In *K. adscendens, K. californica, K. grandiflora, K. peninsularis,* and *K. perennans* the fruiting peduncle is bent sharply at the base and is straight above. *Kallstroemia parviflora* may be as the latter species, or the peduncle is completely straight. It is straight in *K. hintonii* and *K. pennellii* and may be







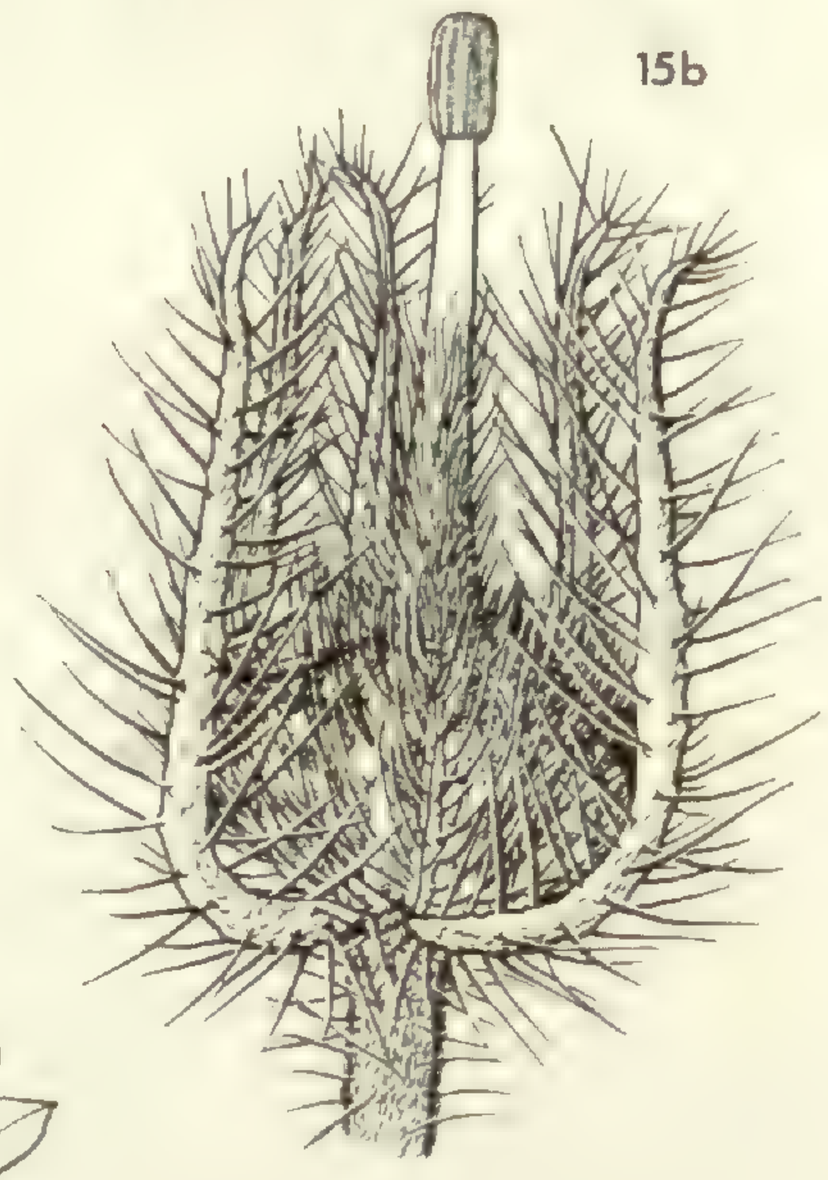


FIG. 14. *Kallstroemia peninsularis: a,* leaf of *Porter 341; b,* fruit of *Wiggins 14454.* FIG. 15. *Kallstroemia perennans: a,* leaf of *Turner 3779; b,* fruit of *McVaugh 8226A.* FIG. 16. *Kallstroemia parviflora: a,* leaf of *Cory 4968; b,* fruit of *Pollard 1295.* FIG. 17. *Kallstroemia hintonii: a,* leaf, *b,* fruit, of *Hinton 12106* (type).

either straight or curved in *K. curta, K. hirsutissima, K. maxima, K. pubescens,* and *K. tucumanensis.*

Fruit. The body of the fruit in most species of the genus is ovoid and three to six millimeters in diameter, but it is broadly ovoid in *Kallstroemia hintonii* (Fig. 17a), *K. hirsutissima* (Fig. 5a), *K. perennans* (Fig. 15a), and *K. standleyi* (Fig. 9a), being four to six millimeters high and six to ten wide. It ranges from glabrous [*K. hintonii* (Fig. 17a), *K. maxima* (Fig. 1a), and *K. tribuloides* (Fig. 11a)] to strigillose [*K. californica* (Fig. 8a), *K. curta* (Fig. 6a), *K. hirsutissima* (Fig. 5a), *K. peninsularis* (Fig. 14a), and *K. pennellii* (Fig. 12a)] or strigose [*K. adscendens* (Fig. 7a), *K. boliviana* (Fig. 10a), *K. grandiflora* (Fig. 13a), *K. parviflora* (Fig. 16a), *K. rosei* (Fig. 2a), *K. standleyi* (Fig. 9a), and *K. tucumanensis* (Fig. 4a)], to occasionally appressed short-pilose [*K. pubescens* (Fig. 3a)], or both hispid and strigose [*K. perennans* (Fig. 15a)].

The length and shape of the beak on the fruit (the persistent style) differs greatly between species. In *Kallstroemia adscendens* (Fig. 7a), *K. curta* (Fig. 6a), *K. hirsutissima* (Fig. 5a), and *K. tucumanensis* (Fig. 4a) the beak is conical and shorter than the fruit body, and in *K. californica* (Fig. 8a) and *K. standleyi* (Fig. 9a) it is cylindrical above with a conical base, but it is shorter than the body. In all other species [*K. boliviana* (Fig. 10a), *K. grandiflora* (Fig. 13a), *K. hintonii* (Fig. 17a), *K. maxima* (Fig. 1a), *K. parviflora* (Fig. 16a), *K. peninsularis* (Fig. 14a), *K. pennellii* (Fig. 12a), *K. perennans* (Fig. 15a), *K. pubescens* (Fig. 3a), *K. rosei* (Fig. 2a), and *K. tribuloides* (Fig. 11a)], it is cylindrical above with a more or less conical base and as long as to longer than the body. Species such as *K. grandiflora, K. hintonii, K. parviflora, K. peninsularis, K. perennans,* and *K. rosei* may have the beak becoming two to three times the length of the fruit body. There is a rough correlation between beak length and flower size.

Pubescence of the beak of the fruit mostly is glabrous or strigose, being usually the same as that on the body of the fruit. *Kallstroemia hirsutissima* and *K. rosei* are unique in that there is a ring of hirsute pubescence surrounding the base of the beak. This pubescence is quite marked in *K. rosei.* The entire beak is hirsute in *K. perennans.*

Another taxonomically useful character of the fruit is the

mericarp. In most species the mericarps are three to five millimeters high and about one millimeter wide, but in *Kallstroemia hintonii, K. perennans,* and *K. standleyi* they may reach a width of from two to two-and-one-half millimeters. The most useful characteristic of the mericarps is in the differences found in their abaxial surfaces. This surface differs from tubercled [*K. curta* (Fig. 6a), *K. grandiflora* (Fig. 13a), *K. hirsutissima* (Fig. 5a), and *K. peninsularis* (Fig. 14a)] to tubercled or rugose [*K. parviflora* (Fig. 16a)], tubercled or rugose, and cross-ridged [*K. pubescens* (Fig. 3a)], tubercled and cross-ridged, [*K. adscendens* (Fig. 7a) and *K. rosei* (Fig. 2a)], tubercled, cross-ridged and slightly keeled [*K. maxima* (Fig. 1a)], cross-ridged and more or less keeled [*K. hintonii* (Fig. 17a), *K. pennellii* (Fig. 12a), and *K. perennans* (Fig. 15a)], tubercled and laterally grooved [*K. tucumanensis* (Fig. 4a)], rugose and margins flattened [*K. boliviana* (Fig. 10a)], or rugose and margins flattened and slightly keeled [*K. tribuloides* (Fig. 11a)]. Four to five oblong, blunt or fungoid tubercles are present in *K. californica* (Fig. 8a) and *K. standleyi* (Fig. 9a) which may become one-and-one-half to two millimeters long and become more prominent as the fruit matures. The pubescence of the abaxial surface is the same as that of the fruit body.

The amount and pattern of pitting on the sides of the mericarp is variable even within the same specimen and is of no diagnostic value. However, there is a certain amount of difference in the shape of the adaxial edge of the mericarp, mirroring the shape of the styliferous axis which persists on the peduncle after the mericarps have fallen. This edge is straight in *Kallstroemia perennans* and *K. standleyi,* curved in *K. tribuloides,* and more or less angled in all the remaining species but *K. pennellii,* where it has not been seen.

HYBRIDIZATION, INTERSPECIFIC RELATIONSHIPS, AND EVOLUTION

Hybridization

In addition to comparative morphology, a commonly used criterion to discern natural relationships in plants is that of hybridization between taxa. Such hybridization may occur in the field, or it may be artificially induced, through crosses in the

experimental garden. The latter type of experimentation has not been done in *Kallstroemia*, but there are two cases of suspected interspecific hybridization in the genus. Evidence for this hybridization occurs in areas where man has transported the parent species and has modified the environment to create new habitats that can be utilized by any resulting hybrids. The majority of instances in which hybridization and introgression have been discovered in plant populations have been detected under such circumstances (Stebbins, 1950).

The first case involves *Kallstroemia maxima* and *K. pubescens*. These two species are sympatric over a wide area of their ranges *(Maps 1 and 4)*, but they appear to be at least partially isolated ecologically. *Kallstroemia pubescens* usually is found at slightly higher elevations and in sandier soils than *K. maxima*, but mixed populations of them have been seen. There is evidence for hybridization between the two only in their southernmost region of overlap, in Colombia and Venezuela *(Map 2)*. Certain herbarium specimens (cited under *K. maxima*) from this area appear to be intermediate between the above species in sepal and fruit characteristics (the two species are very similar vegetatively), and I suspect that these specimens are of hybrid origin.

Examination of the sepals and fruits of *Kallstroemia maxima* and *K. pubescens* with magnification shows these structures to be quite different in the two species (Fig. 1b and 3b). The sepals of *K. maxima* are ovate and clasp the mature fruit, only the scarious margins becoming involute. The sepal trichomes are hirsute, of one length, and usually are appressed toward the sepal apex. The fruit in this species is ovoid and usually is glabrous, occasionally being strigose with short, rigid, curved trichomes. By contrast, in *K. pubescens* the sepals spread from the base of the mature fruit, the margins become sharply involute, and consequently the sepals appear to be linear or linear-lanceolate. The sepal trichomes are hispidulous, spreading stiffly, and of two lengths. They are much finer than those of *K. maxima*. The fruit of *K. pubescens* is more pyramidal than in *K. maxima*, and it is densely pubescent with fine, straight, appressed-pilose trichomes.

These sepal and fruit characters are more or less intermediate in the suspected hybrids. In the latter specimens, the sepals either clasp the mature fruit or spread from it. The amount of involution of the sepal margins is moderate, but it does not reach either

extreme found in one species or the other. Trichomes are variable in length on the same sepal and usually are spreading, not appressed. The sepal trichomes are not as fine or as short as those of *Kallstroemia pubescens*, and not as stout as those of *K. maxima*, but they may be as long as those of the latter species. The shape and tuberculation of the fruit approaches that of *K. maxima*, but fruit pubescence is of the same type as that found in *K. pubescens*. This pubescence is much denser than that sometimes found in *K. maxima*. Microscopic examination of pollen grains stained with acetocarmine following removal from unopened flowers of both the species and the suspected hybrids revealed less than nine per cent malformed grains in collections of each of the three from the same general area. When the pollen was treated with methylene blue, all of the grains were stained, even if malformed. Specimens of the putative hybrids are listed in the taxonomy section following the discussion of *K. maxima*.

In contrast to the above situation where hybridization only is suspected, there is evidence of both hybridization and introgression between *Kallstroemia maxima* and *K. rosei* where their ranges overlap in southwestern Mexico *(Maps 1 and 3)*. However, no plants that could be considered intermediates between the two species have been seen. *Kallstroemia maxima* and *K. rosei* both apparently have been transported to this area during historical times. This introduction, at least in the case of *K. rosei*, presumably is still taking place. The latter species is native to open, disturbed habitats in the pine-oak forests of central Mexico at elevations above about 1000 meters, while *K. maxima* is a more tropical species from the lower elevations of the Caribbean and Central American region. The two species have been brought together mainly in the region of the Río Balsas Basin, where increased cultivation and other disturbances have provided suitable habitats for these species to overlap in their distributions. Before man's intervention, they undoubtedly were allopatric.

The two species are rather similar vegetatively, differing mainly in flower and fruit characters, although *Kallstroemia rosei* tends to be larger in vegetative characters. Characteristically, the fruits of the latter (Fig. 2b) are densely pubescent, the fruit body being strigose with short curved trichomes and with longer, stouter, straight trichomes forming a ring of white, hirsute pubescence around the base of the beak. This ring may be quite striking to

the naked eye. In specimens from this area of overlap, however, the fruits on some individuals are almost glabrous. On others, the fruits vary markedly in the amount of pubescence on the same individual, a situation unknown elsewhere in the range of *K. rosei*. There is also some variation in the amount of involution of the sepal margins in these specimens. Following anthesis, the sepals usually spread from the base of the fruit, and their margins become sharply involute. However, in the suspected introgressants, the margins may fold under, but not nearly to the extent normal for the species. The sepals also occasionally clasp the mature fruit, rather than spread from it.

The fruits of *Kallstroemia maxima* (Fig. 1b) are almost always glabrous, but most of the collections of this species, from its area of overlap with *K. rosei*, are strigose to a greater or lesser extent. However, none of these specimens has the ring of hirsute pubescence surrounding the base of the beak that is found in *K. rosei*. The sepals of *K. maxima* in this area also vary toward those of *K. rosei*. They generally fail to extend beyond the mature mericarps, but here they may reach to the top of the beak. The sepal margins are more involute in these specimens than is true elsewhere, usually only the scarious margins become involuted. However, involution of the sepal margins in *K. maxima* never reaches the extreme of that found in *K. rosei*.

Although the information summarized above suggests the presence of interspecific hybridization in the genus, experimental proof of its existence is lacking. Such proof concerning the compatibility of these species and the isolating mechanisms present between them is desirable, as is more information concerning the geographical relationships of both the species and their suspected hybrids. This vital information, along with cytological studies, undoubtedly will help in interpreting the morphological data at hand. In the absence of genetical evidence, it is thought best to consider these individuals only as suspected hybrids.

Interspecific Relationships

The geographical distribution of the genus suggests that it has arisen somewhere in North America, probably Mexico, which is its present center of diversity and abundance. However, with almost complete lack of a fossil record, it cannot be certain that the

genus did not originate in an area where it is now absent. Although all known members of the *Zygophyllaceae* now inhabit arid or semiarid habitats, it does not necessarily follow that the ancestors of *Kallstroemia* did so as well. It is still open to question whether the ancestors of the present-day species ranged throughout the tropics, evolving species independently in North and South America, or whether they gradually adapted to more arid conditions in the north and have since invaded both arid South America and dry, open, disturbed habitats in the tropics. This question is complicated not only by a lack of knowledge of the genetics and cytology of the genus, but also by the lack of a species or a group of species that can be definitely regarded as primitive. Comparative morphology reveals that the species of North America are more closely related to each other than to any species of South America. Each continental grouping of species shows certain relationships to those of the tropics.

The evidence derived from comparative morphology regarding species relationships in the genus discussed above may be summarized as follows. In North America, *Kallstroemia grandiflora, K. parviflora, K. peninsularis,* and *K. perennans* form a group of closely interrelated species. *Kallstroemia hirsutissima, K. californica,* and *K. standleyi* make up another group in which the latter two species appear to be most closely related. However, *K. hirsutissima* shows close relationships to the Caribbean *K. curta,* and *K. californica* to *K. adscendens* of the Galápagos Islands. The Mexican *K. rosei* is closest to the Caribbean *K. maxima,* while *K. hintonii* does not appear to be closely related to any other species. In South America, *K. boliviana* and *K. tribuloides* are closely related to one another and show relationships to *K. pennellii.* On the other hand, *K. tucumanensis* is very close to the Caribbean *K. pubescens.* The morphological bases for these relationships are discussed under the relevant species.

Evolution

There is paleobotanical evidence for the presence of semiarid vegetation in both the northern and southern hemispheres of the New World during the late Eocene and early Oligocene, but evidence for desert floras in North America before the Pliocene is lacking (Axelrod, 1950, 1958). Desert vegetation types appear to

have developed during the latter epoch through the appearance of more arid communities in the rain shadows of the rising mountain systems in the western area of the continent. Likewise, the desert vegetation of Argentina is surmised to have developed late in the Cenozoic, concomitant with the elevation of the Andean system (Berry, 1928, 1932). The ecological effects of the Andean orogeny began in the Miocene and reached their present maximum in the Quaternary (Simpson, 1965).

A rapid evolution of herbaceous plants during the late Tertiary and Quaternary has coincided with this differentiation and spread of arid and semiarid communities (Stebbins, 1947, 1949; Axelrod, 1950). This great expansion and diversification of herbs appears to have been a direct response to the factors causing a comparatively rapid change toward a warmer, drier climate. Modern desert species have been derived by the gradual adaptation of more mesic ancestors to lowered yearly rainfall, shifting seasonal distribution of rain, and increasing ranges and extremes of temperature (Axelrod, 1950). As has been the case with a number of herbaceous genera, the ancestors of the present-day species of *Kallstroemia* adapted to this increasingly more xerophytic environment by evolving annuals which inhabit areas marked by high summer temperatures and summer rainfall. A principal advantage of the annual habit for these plants has been their ability to pass through the dry season unfavorable to growth as drought-resistant seeds.

The rapid evolution associated with these large climatic changes has involved not only the development of adaptations to drier conditions and the rise of the annual habit, but also has been greatly aided and diversified by the alternate isolation and merging of populations, providing opportunities for increase in genetic diversity through hybridization and introgression (Stebbins, 1949, 1952). Furthermore, the population structure of species in arid and semiarid regions is likely to be more favorable for evolution than that of species in more mesic habitats (Stebbins, 1952). The frequent isolation of small populations offers many situations for genetic change through natural selection and chance fixation. Occasional migration between populations further increases their genetic diversity and offers new gene combinations to the selective action of the environment. Such a population structure is that most favorable to rapid evolution (Wright, 1940).

Populations of *Kallstroemia* characteristically are local and discontinuous. They rarely cover extensive areas, although individuals usually are numerous where found. Exceptions to this pattern are at times found in *K. californica, K. grandiflora* and *K. hintonii,* but such extensive masses of the plants are exceptional. This population structure helps to explain the small amount of phenotypic diversity to be found in most local populations, and the perceptible differences seen between such populations. The genetic makeup of the seed or seeds founding a new population, random genetic drift, and chance interpopulational hybridization, along with vigorous environmental selection, have all acted to produce these differences. On a larger scale, they have led to speciation.

ECONOMIC IMPORTANCE

Although by no means a genus of great economic importance, *Kallstroemia,* and especially *K. maxima,* finds many uses in the native *materia medica* of the areas where it is to be found. It is also a minor forage plant.

In Sonora, Mexico, *Kallstroemia californica* (presumably the herbage) is used in the cure of insect and reptile bites (Rose, 1891).

According to McGinnies (1922), the forage value of *Kallstroemia grandiflora* is excellent, and it is chiefly grazed in the summer. However, another source (Anonymous, 1963, p. 72) states that, it "has very little forage value due to its rough foliage," but it "is a good summer cover crop." The seeds are eaten by quail in the summer and fall (Griner, 1940). These reports are from Arizona. Watson (1889, p. 43), writing of specimens from Sonora, Mexico, states that the pollen of this plant is injurious to the eyes, and therefore the plant is called *Mal de Ojos* (bad for the eyes).

Kingsbury (1964) cites a report of *Kallstroemia hirsutissima* poisoning cattle under natural conditions, and sheep and goats under experimental conditions. The toxic principle is unknown.

As mentioned above, *Kallstroemia maxima* has a number of medicinal uses throughout its range. In Jamaica, a salve is made of the plant by mixing it with suet, which is effective against ringworm (Sloane, 1707). A poultice is used for various cutaneous

afflictions in Cuba (Baillon, 1875; Gomez de la Maza, 1889) and Surinam (Westroüen van Meetenen, 1883). In Venezuela (Perez Arbeláez, 1956) and Costa Rica, this is used also to bring boils and similar sores to a head. In the latter country, the infusion and decoction purportedly is effective against paralysis, tetanus, and spasms (Pittier, 1957), and in Colombia the infusion is used as a diuretic (Perez Arbeláez, 1956).

Kallstroemia maxima is eaten by herbivores in Jamaica (Browne, 1756) and Cuba (Richard, 1845) and is the only species in the genus reported to be eaten by man. According to Standley (1928), the plant sometimes is cooked and eaten as a potherb in El Salvador, and Perez Arbeláez (1956) reports this use in Colombia. This may be the case, but it probably results from the close resemblance of *K. maxima*, at least to the native user, to *Portulaca oleracea* L. *(Portulacaceae)*, a common potherb throughout Latin America. These plants grow under the same conditions and are found together. They superficially resemble one another vegetatively, and are known universally throughout their ranges in Latin America by the same common name, *Verdolaga.*

In New Mexico, "the Spanish New Mexicans say that the powdered roots [of *Kallstroemia parviflora*–reported as "*K. brachystylis*"], when soaked in warm water, make a good wash for sore eyes and swollen gums. Also if taken as a tea it is an excellent remedy for fever, stomach trouble and dysentary" (Anonymous, 1963, p. 72). Perhaps the root infusion would be efficacious in the case of *K. grandiflora* pollen in the eyes! Lopez (1948), writing from Chihuahua, Mexico, states that this species "es buena para el estomago" (is good for the stomach). In Peru *K. parviflora* is used as forage by stock (Macbride, 1949).

According to Standley (1940), *Kallstroemia pubescens* in Guatemala is utilized as a remedy for kidney stones. The species also is appreciated in Ghana, Africa, where it was long ago introduced: "The leaves are used to cure constipation. They are powdered in a morter with palm nuts and drunk as soup in 3 doses. This is also believed to induce conception. The leaves are put into water, salt is added, and when they have been boiled, the liquor is drunk as another cure for constipation" (Irvine, 1930, p. 419).

In Argentina both *Kallstroemia tribuloides* and *K. tucumanensis* are eaten by herbivores (Ruíz Leal, 1947, 1951). The former

species apparently is the only one in the genus, except perhaps for *K. grandiflora,* which has been raised as an ornamental: "The seeds of this plant may be raised on a hot-bed, and when the plants have grown 2 or 3 inches, they may be planted out in the open border in a sheltered situation, in the month of May" (Don, 1831, p. 769).

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Taxonomic History

Since the the foundation of the genus by Scopoli in 1777, most of the published material on *Kallstroemia* has been concerned with either distributional and ecological information or the description of new species. The most recent work of a revisional nature was done by Rydberg in 1910 and covered North America only. It is now very much out of date.

The following list is a chronological taxonomic history of the genus.

1696: Sloane published the first notice of the plant later to be called *Kallstroemia maxima*, "Tribulus terrestris major flore maximo odorato." Thus, the epithet *maxima* is based not on floral size, as many have assumed (e.g., Macfadyen, 1837), but on floral odor.

1707: The first illustration of a *Kallstroemia (K. maxima)* was published by Sloane.

1753: Linnaeus described *Tribulus maximus (= Kallstroemia maxima)* from Jamaica, citing Sloane in the protologue.

1777: Scopoli published *Kallstroemia*, basing it on "*Tribulus maximus* Loefl." (= *Tribulus maximus* L.). The derivation of the name was never explained. Some authors suggest it was compounded from "Greek Kallos, beautiful, and Stroemia, a genus of Capparidaceae" (Jepson, 1936, p. 437), while others believe it to be "in honor of *Kallstroem*, obscure contemporary of Scopoli" (Munz, 1959, p. 159). Scopoli made no combinations in the genus.

1818: Nuttall described *Tribulus trijugatus (= Kallstroemia maxima)* from Georgia.

1825: The fundamental differences between fruits of *Tribulus maximus* and those of the other known species of *Tribulus* were recognized by A. Jussieu. He stated that perhaps a new genus should be based on the former species, apparently unaware that Scopoli already had done so on the same basis 48 years previously.

1826: The genus *Ehrenbergia* was described by von Martius from Brazil.

1827: Von Martius published *Ehrenbergia tribuloides (= Kallstroemia tribuloides)*, correctly recognizing its affinities with *Tribulus*, but apparently he was unaware that it was actually the second known species of *Kallstroemia*.

1827: Sprengel published *Tribulus brasiliensis (= Kallstroemia tribuloides)* from Brazil, basing it on *Ehrenbergia tribuloides*. *Ehrenbergia* Mart. is a later homonym for a genus erected by Sprengel in the Rubiaceae.

1828: Reichenbach was the first to recognize and use the name *Kallstroemia* since its publication.

1831: George Don described *Tribulus pubescens (= Kallstroemia pubescens)* from the "Cape Coast," now Ghana. This is the only species of *Kallstroemia* known to occur outside the New World, also being introduced to Nigeria and India.

1834: Wight and Arnott indicated that *Kallstroemia* was distinct from *Tribulus*, but they made no new combinations in the genus.

1835: The genus *Heterozygis* was erected by Bunge, who based it on *Tribulus maximus*. He published no new combinations.

1836: The first combination was made in *Kallstroemia*, *K. cistoides*, by Endlicher. However, the species is actually a *Tribulus*, *T. cistoides*.

1837: Macfadyen published *Tribulus decolor (= Kallstroemia maxima)* from Jamaica.

1837: Meisner published *Kallstroemia tribulus (= Kallstroemia maxima)*, basing it on *Tribulus maximus*.

1838: Hooker and Arnott were the first to correctly place a species, *K. maxima,* in *Kallstroemia.*

1840: Rafinesque published *Tribulus dimidiatus (= Kallstroemia maxima),* based on *T. trijugatus.*

1840: The combination *Kallstroemia tribuloides* was published by Steudal, who wrongly attributed it to Wight and Arnott.

1841: Steudal published *Tribulus trijugus,* an orthographic error for *T. trijugatus.*

1849: Robert Brown recognized the basic differences in the fruits of *Kallstroemia, Tribulopis,* and *Tribulus.*

1849: J. D. Hooker published *Kallstroemia minor (=K. pubescens)* from Ghana, basing it on the same type as *Tribulus pubescens.*

1852: Gray described *Kallstroemia grandiflora* from Arizona and *K. grandiflora* var. *detonsa (= K. grandiflora)* from New Mexico.

1854: *Tribulus adscendens (= Kallstroemia adscendens)* was described from the Galápagos Islands, Ecuador, by Andersson.

1859: Grisebach divided *Tribulus* into two sections, *Eutribulus* and *Kallstroemia,* basing the division on characters of the fruit.

1861: Andersson published the combination *Tribulus maximus* var. *adscendens (= Kallstroemia adscendens).*

1862: J. D. Hooker treated *Kallstroemia* and *Tribulopis* as subgenera of *Tribulus.*

1867: Hooker now placed *Kallstroemia* and *Tribulopis* as sections of *Tribulus.*

1868: *Tribulus maximus* var. *minor (= Kallstroemia pubescens)* was described by Oliver.

1872: Baillon argued that the differences between *Kallstroemia* and *Tribulus* were not sufficient to warrant the separation of the former from *Tribulus.*

1876: *Tribulus californicus (= Kallstroemia californica)* was described by Watson from Baja California, Mexico.

1876: Brewer and Watson published the combination *Tribulus grandiflorus (= Kallstroemia grandiflora)* erroneously ascribing it to Bentham and Hooker.

1877: Kellogg described *Tribulus fisheri (= Kallstroemia grandiflora)* from Sonora, Mexico.

1887: After long treating them as genera separate from *Tribulus,* Gray now indicated that *Kallstroemia* and *Tribulopis* should be considered as synonyms of the former because of the supposed close resemblances between species of *Tribulus* and *Kallstroemia californica.*

1890: Engler divided *Kallstroemia* into two sections, *Eukallstroemia* and *Thamnozygium,* the former with nine species, the latter with two species. He also placed *Tribulopis* as a synonym of *Kallstroemia,* and seven of the species in *Eukallstroemia* and both those in *Thamnozygium* were new combinations from this genus and *Tribulus.* The remaining two species in section *Eukallstroemia, Kallstroemia maxima* and *K. tribuloides,* are the only ones at present considered actually to belong in the genus.

1894: Sessé and Mociño's *Tribulus tuberculatus (= Kallstroemia maxima)* was described from Cuba.

1895: Vail published the combination *Kallstroemia californica.*

1897: *Kallstroemia brachystylis (= K. californica)* was described by Vail from New Mexico.

1897: Gray recognized three sections in *Tribulus,* two of which constituted *Kallstroemia,* the other being *Tribulus s. str.*

1897: Robinson published the combination *Tribulus brachystylis (= Kallstroemia californica).*

1898: Kuntze described *Tribulus maximus* var. *roseus* (= *Kallstroemia boliviana)* from Bolivia.

1898: *Kallstroemia parviflora* was described from Texas by Norton.

1900: Cockerell described *Kallstroemia grandiflora* var. *arizonica* (= *K. grandiflora)* from Arizona.

1902: The combination *Kallstroemia adscendens* was published by Robinson, reversing his previous belief that *Kallstroemia* should be considered a synonym of *Tribulus.*

1903: Vail described *Kallstroemia hirsutissima* from New Mexico.

1910: Rydberg, in the most complete revision of *Kallstroemia* to date, described six new species in the genus. These were *K. canescens* (= *K. maxima)* from Sinaloa, Mexico; *K. caribaea* (=*K. pubescens)* from Montserrat, West Indies; *K. glabrata* (= *K. pubescens)* from Guerrero. Mexico; *K. intermedia* (= *K. parviflora)* from Texas; *K. longipes* (= *K. pubescens)* from Sinaloa; and *K. rosei* from Morelos, Mexico.

1913: Britton and Brown chose *Tribulus maximus* as the lectotype species of *Kallstroemia.*

1913: *Kallstroemia laetevirens* (= *K. parviflora)* was described from New Mexico by Thornber.

1913: Rydberg described *Kallstroemia curta* from Curaçao, West Indies.

1924: *Kallstroemia incana* (= *K. curta)* was described by Rydberg from Hispaniola, West Indies.

1931: Engler maintained his subgeneric classification of *Kallstroemia,* with the exception that 18 species were now included in section *Eukallstroemia* and two in section *Thamnozygium.*

1935: L. O. Williams described *Kallstroemia hirsuta* (=*K. perennans)* from Texas, not realizing that the name was a later homonym of a combination made by Engler in 1890.

1936: Standley described *Kallstroemia boliviana* from Bolivia. Although Standley was considered to be an expert on the *Zygophyllaceae,* this was the only species he ever published in this genus.

1939: *Kallstroemia tucumanensis* was described from Argentina by Descole, O'Donell, and Lourteig.

1939: Kearney and Peebles published the combination *Kallstroemia californica* var. *brachystylis* (= *K. californica).*

1950: Turner published *Kallstroemia perennans,* a new name for William's *K. hirsuta.*

1955: The combination *Kallstroemia pubescens* was published by Dandy.

Material Examined

The first set of my collections has been deposited in the Gray Herbarium of Harvard University. Specimens from 31 institutions have been studied and many of them are cited by herbarium abbreviations under each taxon. These are the standardized abbreviations of Lanjouw and Stafleu (1964), except for the following, which are not included in their publication:

ENAG Escuela Nacional de Agricultura y Ganadería. Managua, Nicaragua.
MAGN Ministerio de Agricultura y Ganadería, Managua, Nicaragua.
USMG Universidad de San Marcos, Guatemala City, Guatemala.

Taxonomic Treatment

Kallstroemia Scop., Introd. 212. 1777. TYPE SPECIES: *Tribulus maximus* L. [*Kallstroemia maxima* (L.) Hook. & Arn.].

Ehrenbergia Mart., Nov. Gen. Sp. Brasil. 2:72. 1826. Not *Ehrenbergia* Spreng., Neue Entdeck. 2:129. 1821. TYPE SPECIES: *Ehrenbergia tribuloides* Mart. [*Kallstroemia tribuloides* (Mart.) Spreng.].

Heterozygis Bunge, Mem. Acad. Sav. Etr. St. Petersb. 2:82. 1835. TYPE SPECIES: *Tribulus maximus* L.

Annual or occasionally perennial herbs. *Stems* herbaceous to suffrutescent, diffusely branched, prostrate to decumbent or ascending; spreading radially from a thick, fibrous central tap root to 1 m or more long and about 1 m high, branching primarily from basal nodes; terete, somewhat succulent, becoming striate on drying, yellow-green to reddish, drying yellow, fibrous, tough, nodes somewhat swollen; densely pubescent to glabrate, hirsute or hispid and sericeous, rarely only sericeous and strigose, trichomes white, gray, or yellow, directed apically or rarely retrorse. *Stipules* 2, interpetiolar, foliaceous, narrowly to broadly falcate, 3–10 mm long, 1–3 mm wide; acuminate, ciliate, pubescent, trichomes as on stem; erect to spreading, persistent. *Leaves* opposite, elliptical to broadly obovate, 1–8.5 cm long, 1.5–5 cm wide, slightly succulent, one of each pair alternately smaller or sometimes abortive; abruptly even-pinnate, petiole usually shorter than leaflets; rachis terminating in a foliaceous, subulate, apiculate, pubescent mucro ca. 1 mm long; petiole and rachis pubescence as on stem. *Leaflets* 2–10 pairs, opposite, entire, elliptical to broadly oblong or obovate, apex acute to obtuse, mucronate, apiculate, base oblique to inequilateral; 3–29 mm long, 1.5–17 mm wide, somewhat unequal in size, those on one side of rachis slightly smaller, lowest pair markedly unequal, terminal pair pointed forward and more falcate; pubescent to glabrate, appressed-hirsute or rarely hispid or sericeous, margins and veins more or less sericeous, usually ciliate; margins flat to occasionally inrolled; venation reticulate; petiolule 1 mm long or less. *Peduncles* pseudoaxillary, more or less thickened distally, pubescence as on stems; erect at anthesis, reflexed in bud and following anthesis; longer or shorter than subtending leaves, 2–105 mm long in flower and fruit; curved, straight, or bent sharply at base and straight above in fruit. *Flowers* solitary, hypogynous, pentamerous or rarely hexamerous, perfect, regular, polypetalous, syncarpous, 7–60 mm in diameter, appearing alternately on stem. *Sepals* 5(–6), foliaceous, free, inserted at base of receptacle, imbricate in bud; lanceolate to broadly ovate, 2–16 mm long, 1–4 mm wide, concave, margins scarious, apex acute, apiculate; pubescent, hirsute or hispid and strigose, or occasionally sericeous or hirsute; scarious margins or entire sepal usually becoming involute, occasionally shriveling and turning brown; clasping or spreading from base of mature fruit; persistent or rarely caducous. *Petals* 5(–6), free, convolute in bud, alternating with and as long or usually longer than sepals, 3–34 mm long, 1.5–20 mm wide, white to bright orange, base same or green to red, drying white to orange; elliptical to broadly obovate, apex rounded or truncate, entire to irregularly notched, veins prominent; spreading hemispherically, fugaceous, usually marcescent. *Disc* fleshy, obscurely 10(–12)–lobed. *Stamens* 10(–12), inserted in 2 whorls in disc; 5 opposite petals exterior, somewhat longer, adnate basally to petals; 5 opposite sepals shorter, subtended to exterior by a small bilobed gland; shorter than petals, 2/3 as long to slightly longer than style. *Filaments* filiform, subulate, or rarely winged at base, same color as petal base. *Anthers* globose or ovoid to linear-oblong or rarely linear, bilobed, sub-basifixed to versatile, yellow

through orange to red, less than 1–2 mm in diameter, or 2–4 mm long; longitudinally dehiscent, introrse, those opposite sepals rarely abortive. *Pollen* spherical, polyforate, yellow through orange to red. *Ovary* superior, sessile, 10(–12)-lobed and -loculed, globose or ovoid and 1–3 mm in diameter, or occasionally conical or pyramidal and 2–4 mm high; glabrous to pubescent, strigose, strigillose, or rarely short-pilose or hispid and strigose. *Ovules* 1 per locule, pendulous, anatropous, placentation axile, sometimes 1 or more aborting. *Style* 1, cylindrical to broadly conical, less than 1–8 mm long, more or less 10(–12)-ridged, persisting to form beak on fruit. *Stigma* capitate, oblong, or clavate, less than 1–7 mm long, terminal or rarely extending down almost to base of style, 10-ridged or -lobed, papillose or rarely coarsely canescent, silvery. *Fruit* 10 (–12)-lobed, ovoid, occasionally conical, or rarely pyramidal, 3–6 mm in diameter or 3–6 mm high and 3–10 mm wide; glabrous to pubescent, strigose, strigillose, or rarely short-pilose or hispid and strigose; at maturity dividing septicidally and separating from a persistent styliferous axis into 10(–12) or occasionally fewer mericarps. *Beak* cylindrical to conical, base more or less conical, 1–18 mm long, glabrous to pubescent. *Mericarps* unilocular, 1-seeded, obliquely triangular, laterally wedge-shaped, 3–5 mm high, 1–2.5 mm wide; abaxially more or less tuberculate or rugose, occasionally also cross-ridged or keeled, glabrous to pubescent; sides glossy, more or less pitted; adaxial edge straight to conspicuously angled. *Seeds* oblong-ovoid, obliquely pendulous from apex of central angle, germination epigeal; testa smooth, white, membranaceous; embryo straight, cotyledons ovoid, radical conical, superior, epicotyl rudimentary; endosperm none.

Key to the Species of Kallstroemia[1]

[1] Information concerning geographical distribution is approximate only and is included primarily for the convenience of the user of the key. The pubescence types as used in the key are defined as follows: hirsute (trichomes long, coarse, spreading, and moderately stiff), hispid (trichomes long, stiff, spreading, and rigid), hispidulous (trichomes very short, stiff, spreading, and rigid), sericeous (trichomes long, fine, appressed, and slightly wavy), short-pilose (trichomes short, soft, and straight), strigose (trichomes short, slightly curved, appressed, and rigid), and strigillose (trichomes very short, slightly curved, appressed, and rigid).

1. Leaves obovate, terminal leaflets of mature leaves largest.
   2. Mature mericarps with 4–5 blunt elongate tubercles to 1.5 mm long; sepals usually deciduous; stems hirsute and strigose (southwestern United States and northern Mexico; Fig. 8a, 8b) ..... 8. *K. californica*.
   2. Mature mericarps rugose to tubercled, cross-ridged, or keeled, tubercles never elongate; sepals persistent; stems hirsute and sericeous.
      3. Ovary and fruit body glabrous or rarely strigose, style and beak glabrous, stigma capitate; sepals hirsute (Caribbean region, southeastern coastal United States, tropical Mexico to northern South America; Fig. 1a, 1b) ..... 1. *K. maxima*.
      3. Ovary and fruit body pubescent, style and beak glabrous to pubescent, stigma clavate, oblong, or if capitate then style hirsute at base or fruit body appressed short-pilose; sepals hirsute and strigose, or hispidulous.
         4. Flowers 2–3.5 cm in diameter, style as long or longer than conical ovary, beak as long or longer than fruit body.

5. Sepals clasping and almost entirely covering mature mericarps, only scarious margins becoming involute; beak ca. as long as fruit body, strigose; stigma oblong; peduncles longer than subtending leaves; leaflets sericeous (Bolivia and Peru; Fig. 10a, 10b) ..... 10. *K. boliviana.*

5. Sepals spreading from base of mature fruit and curving upward, margins becoming strongly involute; beak ca. twice as long as fruit body, base hirsute; stigma capitate; peduncles usually shorter than subtending leaves; leaflets appressed-hirsute and sericeous (Mexico; Fig. 2a, 2b) ..... 2. *K. rosei.*

4. Flowers 1.5 cm or less in diameter, style as long or usually shorter than globose, ovoid, or pyramidal ovary, beak shorter than fruit body.

6. Sepals clasping mature fruit, only scarious margins becoming involute; fruit broadly ovoid, 4–5 mm high, 6–8 mm wide, beak hirsute (southwestern United States and northern Mexico; Fig. 5a, 5b) ..... 5. *K. hirsutissima.*

6. Sepals spreading from base of mature fruit, margins becoming strongly involute; fruit ovoid, 3–6 mm in diameter, beak strigose, appressed short-pilose, or glabrous.

7. Sepals hirsute and strigose; stigma clavate; fruit strigillose, beak 1.5–2 mm long and widely conical (Cuba, Hispaniola, and Netherlands Antilles; Fig. 6a, 6b) ..... 6. *K. curta.*

7. Sepals hispidulous with trichomes of two lengths; stigma capitate; fruit appressed short-pilose or strigose, beak narrowly conical or cylindrical above.

8. Flowers 9–15 mm in diameter, petals 6–11 mm long and 5–8 mm wide; ovary pyramidal, 3–5 mm long including style; fruit densely appressed short-pilose, beak 5–8 mm long (Caribbean region, tropical Mexico to Peru, West Africa, India; Fig. 3a, 3b) ..... 3. *K. pubescens.*

8. Flowers 4–8 mm in diameter, petals 3–5 mm long and 2–3 mm wide; ovary ovoid, ca. 1 mm in diameter, style 1 mm long; fruit strigose, beak 2–3.5 mm long (Argentina and Bolivia; Fig. 4a, 4b) ..... 4. *K. tucumanensis.*

1. Leaves elliptical, middle leaflets of mature leaves largest.

9. Stem pubescence retrorse; stigma extending from along upper 1/3 to ca. entire length of style, surface papillose (southern Baja California, Mexico; Fig. 14a, 14b) ..... 14. *K. peninsularis.*

9. Stem pubescence antrorse; stigma usually terminal and surface papillose, but if extending along upper 1/3 of style then surface coarsely canescent with short gray trichomes.

10. Flowers 1 cm or less in diameter, style stout, conical, shorter than ovary.

11. Leaflets 2–3 pairs; sepals persistent; peduncles longer than subtending leaves in fruit; stems hirsute and sericeous (Galápagos Islands, Ecuador; Fig. 7a, 7b) ..... 7. *K. adscendens.*

11. Leaflets 3–7 pairs; sepals usually deciduous; peduncles shorter than subtending leaves in fruit; stems hirsute and strigose (southwestern United States and northern Mexico; Fig. 8a, 8b) ..... 8. *K. californica.*

10. Flowers 1 cm or more in diameter, style conical to cylindrical, longer than ovary.
    12. Ovary and fruit glabrous.
        13. Flowers 3–6 cm in diameter; petals white, aging yellow, base yellow-green or rarely red; filaments winged at base; stems hirsute and sericeous, leaflets 5–7 pairs (Michoacán, Mexico; Fig. 17a, 17b) ..... 17. *K. hintonii.*
        13. Flowers 1.5–2.5 cm in diameter; petals orange, base sometimes darker; filaments filiform to subulate; stems sericeous, leaflets 3–6 pairs (Argentina, Bolivia, and Brazil; Fig. 11a, 11b) ..... 11. *K. tribuloides.*
    12. Ovary and fruit pubescent.
        14. Sepals sericeous, spreading from base of mature fruit, margins becoming strongly involute; beak from ca. 1/2 as long to as long as fruit body; mature mericarps with several elongate blunt or slightly fungoid tubercles to 2 mm long (Oaxaca, Mexico; Fig. 9a, 9b) ..... 9. *K. standleyi.*
        14. Sepals hispid and strigose, or if sericeous then clasping mature mericarps and margins not becoming involute; beak from as long as fruit body to three times as long; mature mericarps rugose to tuberculate or cross-ridged and keeled, tubercles never elongate.
            15. Fruit densely hispid and strigose; stigma extending along upper 1/3 of style, surface coarsely canescent with short gray trichomes (southwestern Texas; Fig. 15a, 15b) ..... 15. *K. perennans.*
            15. Fruit strigose or strigillose; stigma terminal, papillose, silvery.
                16. Sepals sericeous, clasping mature mericarps, margins not becoming involute; stems strigose (Peru; Fig. 12a, 12b) ..... 12. *K. pennellii.*
                16. Sepals hispid and strigose, extending upward beyond mericarps, shriveling and turning brown, margins becoming strongly involute; stems hirsute and sericeous, or hispid and strigose.
                    17. Flowers 2–6 cm in diameter, petals 10–34 mm long and 7–22 mm wide; stigma clavate, 2–3 mm long; peduncles 3–10.5 cm long in fruit (southwestern United States, northwestern and western Mexico; Fig. 13a, 13b) ..... 13. *K. grandiflora.*
                    17. Flowers 1–2.5 cm in diameter, petals 5–11 mm long and 3.5–6 mm wide; stigma oblong, ca. 1 mm long; peduncles 1–4 cm long in fruit (central and southwestern United States, northeastern and central Mexico, Peru; Fig. 16a, 16b) ..... 16. *K. parviflora.*

1. **Kallstroemia maxima** (L.) Hook. & Arn., Bot. Beechey 282. 1838

The author combination usually is attributed to "Torr. & Gray," Fl. N. Amer. 1:213. 1838. Publication of the latter's Part 2, pp. 185–360, however,

took place in October, 1838 (Jackson, 1893), while Part 6, pp. 241–288, of Hooker and Arnott was published before August, 1838 (Marshall, 1950). The combination also occasionally is attributed to "Wight & Arn., Prodr. 1:145. 1834." However, Wight and Arnott never made this combination. They wrote, "*Kallstroemia*, Scop. (containing *Trib. maximus*, Lin. and *Ehrenbergia tribuloides*, Mart. . . .", thus recognizing *Kallstroemia* as distinct from *Tribulus*, but not proposing any new combinations in the genus.

Tribulus maximus L., Sp. Pl. 1:386. 1753. TYPE: According to Fawcett and Rendle (1920, p. 166), "Specimen from Hort. Cliff. in Herb. Mus. Brit., and from Browne in Herb. Linn., the latter named by Linnaeus." The former should be taken as the holotype, as Browne's herbarium was not acquired by Linnaeus until 1758 (Stern, 1957). Linnaeus also cited names from Sloane and Ray in his protologue, but the specimen at BM appears to be the only one actually studied by him. This specimen has not been seen.

Tribulus trijugatus Nutt., Gen. 1:277. 1818. TYPE: Georgia, Chatham Co.: Savannah, *Thomas Nuttall s. n.* (holotype presumably at BM, not seen; PH, isotype).

Kallstroemia tribulus Meisn., Pl. Vasc. Gen. 2:43. 1837. *nom. superfl.* Based on "*Tribulus maximus* Loefl.", cited as a synonym.

Tribulus decolor Macfad., Fl. Jamaica 186. 1837. *nom. superfl.* Based on *T. maximus* L., cited as a synonym.

Tribulus dimidiatus Raf., Autikon Bot. 176. 1840. *nom. superfl.* Based on *T. trijugatus* Nutt., cited as a synonym.

Tribulus trijugus Steud., Nom. Bot. Ed. 2. 2:699. 1841. *nom. superfl.* Orthographic error for *T. trijugatus* Nutt.

Tribulus tuberculatus Ses. & Moc., Fl. Mex. Ed. 2. 109. 1894. TYPE: Cuba, near Havana, *Martín Sessé* (holotype presumably at MA, not seen).

Kallstroemia canescens Rydb. in Vail & Rydb., N. Amer. Fl. 25:113. 1910. TYPE: Mexico, Sinaloa: Rosario, 7 July 1897. *J. N. Rose 1547* (US, holotype; GH, NY, isotypes).

Annual; *stems* prostrate to decumbent, to 1 m or more long, sericeous and sparingly hirsute with apically-directed white or yellow trichomes, becoming glabrate; *stipules* 3–5 mm long, ca. 1 mm wide; *leaves* obovate, 1–6 cm long, 1.5–5 cm wide; *leaflets* 3–4 (–6) pairs, broadly oblong to elliptical, appressed-hirsute to glabrate, margins and veins sericeous, 5–29 mm long, 3–14 mm wide, terminal pair usually largest; *peduncles* at first shorter than subtending leaves, equalling them or longer in fruit and straight or curved, little thickened distally, 1–5 cm long; *flowers* pentamerous, 7–25 mm in diameter; *sepals* ovate, 3–8 mm long, 2–3 mm wide, as long or little shorter than petals, hirsute, trichomes appressed to spreading, in flower ca. as long as style, in fruit clasping but not entirely covering mature mericarps and shorter than beak, only scarious margins becoming involute, persistent; *petals* white through yellow to pale orange, base white to yellow-green or green or rarely red, often brighter than distal portion, fading white to bright orange, obovate, 5–12 mm long, to 10 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid or rarely linear, ca. 1 mm in diameter, they and pollen yellow or red-orange; *ovary* ovoid, ca. 1 mm in diameter, usually glabrous but occasionally strigose at base or rarely to base of style; *style* 2–3 mm long, cylindrical, base slightly conical; *stigma* capitate, ca. 1 mm long, obscurely 10-lobed, papillose; *fruit* ovoid, 5–6 mm in diameter, usually glabrous but occasionally strigose at base or rarely to base of beak; *beak* 3–7 mm long, usually ca. as long as fruit body, glabrous, cylindrical, base widely conical; *mericarps* 3–4 mm high, ca. 1 mm wide, abaxially tubercled cross-ridged and slightly keeled, sides pitted, adaxial edge angled. *Fig. 1a, 1b. Map 1.*

FLOWERING DATES. Flowers year around, whenever sufficient moisture is available for seed germination and plant growth.

DISTRIBUTION AND HABITAT. Disturbed areas from sea level to about 1350 m, usually at lower elevations, from northern South America north through the Caribbean to South Carolina and through western Central America to Sinaloa on the west and Tamaulipas on the east coast of Mexico, also introduced into Texas *(Map 1)*. Sympatric with *Kallstroemia curta, K. hintonii,* and *K. standleyi,* and over much of its range with *K. pubescens;* to the northwest overlapping slightly with *K. californica, K. grandiflora, K. hirsutissima,* and *K. parviflora,* and more so with *K. rosei.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia maxima* is easily recognized by its combination of obovate leaves, usually three to four pairs of leaflets, white to pale orange flowers (the petal bases are white to green or rarely red) 7–25 mm in diameter, hirsute sepals which clasp the mature mericarps, only the scarious margins of the sepals becoming involute, usually glabrous ovaries and fruits, and a capitate obscurely ten-lobed stigma. *Kallstroemia pubescens* and *K. rosei* are the only species from the same area with which it is likely to be confused. However, in the latter species, the sepals spread from the base of the mature fruit, and the sepal margins become sharply involute, thus the sepals appear to be linear or linear-lanceolate. The sepal pubescence in *K. pubescens* is hirsutulous, in *K. rosei* hirsute and strigose; and both have pubescent fruits. There is some overlap in flower diameter between these three species, but the flowers in *K. maxima* on the average are larger than in *K. pubescens* and smaller than in *K. rosei.* The same relationship holds for overall plant size, and *K. maxima* also tends to be less decumbent than *K. rosei.* In addition, in areas where *K. maxima* and *K. rosei* overlap in their distributions, and in localities where both *K. maxima* and *K. pubescens* are to be found, petal color is yellow to orange in *K. maxima* and white in the other two species.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. TEXAS. Washington Co.: Brenham, *Lehmann,* 10 July 1934 (GH, TEX). SOUTH CAROLINA. Charleston Co.: Charleston, *Elliott s. n.* (PH). GEORGIA. Chatham Co.: Savannah, *Backman s. n.* (PH). McIntosh Co.: Doboy I., *H. H. Smith 2348* (F). Glynn Co.: streets, Brunswick, near sea level, *Harper 1529* (BM, F, GH, MO, NY, US). FLORIDA. Escambia Co.: waste places, Pensacola, *Mohr,* July 1874 (F). Duval Co.: Jacksonville, *Williamson,* Aug

1894 (PH). St. Johns Co.: St. Augustine, dooryards, etc., *Curtiss 6424* (GH, MO, NY, SMU, UC, US). Hillsborough Co.: Tampa, waste ground, *Barnhart 2235* (NY). Monroe Co.: Key West, low waste places, *Curtiss 416* (BM, F, MO, NY, PH, US).

MEXICO. SINALOA: Mazatlán, *González Ortega 7295* (CAS, F, MEXU, US); near Rosario, sand dunes, *Rose, Standley & Russell 14641* (GH, NY, US). NUEVO LEON: Monterrey, *Black 39–7458* (NY). TAMAULIPAS: near Tampico, ca. 15 m, *Palmer 116* (BM, CAS, F, GH, MO, NY, US). NAYARIT: near Acaponeta, cultivated fields, *Rose, Standley & Russell 14400* (F, GH, NY); near San Blas. *Ferris* 5388 (DS, GH, MEXU, US). JALISCO: outskirts of Ameca, roadside, 1225 m, *McVaugh 18579* (MICH); Puerto Vallarta, *Howell 10352* (CAS, POM). COLIMA: Colima, *Palmer 98* (US); Manzanillo, edge of dusty street, *Porter 1481* (GH, MEXU). SAN LUIS POTOSI: El Pujal, 100 ft, *Chase 7510* (ARIZ, F, GH, MICH, MO, NY); 15 mi E of Valles, flat bushy area, *Waterfall & Wallis 14310* (F, SMU). MICHOACAN: Aguililla, llano, 900 m, *Hinton 15153* (DS, GH, MICH, NY, RSA, US); Apatzingán, dry waste ground, 1200 ft, *Leavenworth & Hoogstraal 1423* (F, GH, MICH, MO, NY). MEXICO: Vigas, hill, 1080 m, *Hinton 4763* (BM, GH). MORELOS: Puente de Ixtla, *Rose, Painter & Rose 9436* (US); near Yautepec, pedregal, *Rose, Painter & Russell 8598* (MEXU, NY, US). VERACRUZ: Cuitláhuac, *Matuda 1420* (DS, GH, MICH, MO, NY); Mocambo, in road to beach, *Porter 1461* (CAS, DS, GH, MEXU). GUERRERO: Atoyac, plain, *Hinton 14575* (ARIZ, LL, NY, PH, TEX, US); 1 mi E of Acapulco, sandy flat above Playa Hornos, *Barkley 14084* (CAS, DS, F, GH, MEXU, MO, PH, POM, RSA, SMU, TEX, UC). OAXACA: Hacienda de Guadalupe, 1650 m, *Conzatti 2190* (F, GH, MEXU); 2 km S of Niltepec, clay loam, *King 1777* (MICH, NY, TEX, UC). TABASCO: San Juan Bautista, cultivated areas, *Rovirosa 160* (PH, US); between San Juan Bautista and Paso del Tierra Colorado, *Rovirosa 567* (NY, PH, US). CHIAPAS: between Mazapa and Motozintla, 1200 m, *Matuda 4831* (GH, LL). CAMPECHE: Ciudad del Carmen, *Mell 2074* (NY, US); Tuxpeña, *Lundell 1217* (ARIZ, DS, F, GH, LL, MEXU, MICH, MO, NY, UC, US). YUCATAN: Chichen Itzá, *Steere 1022* (BM, MEXU, MICH, MO, NY); Izamal, *Gaumer 462* (BM, CAS, DS, F, GH, MICH, MO, NY, PH, SMU, UC, US, WIS). QUINTANA ROO: Chichankanab, *Gaumer 1780* (BM, CAS, DS, F, PH, UC, US).

GUATEMALA. PETEN: near La Libertad, *Aguilar H. 175* (F, MICH, MO). HUEHUETENANGO: near Cuilco, thickets along Río Cuilco, 1350 m, *Steyermark 50759* (F, US). QUICHE: without locality, *Aguilar G. 492* (F). IZABEL: near Puerto Barrios, open bank, sea level, *Standley 25147* (GH, US). SAN MARCOS: Ocós, sands, 1–2 m, *Steyermark 37853* (F). RETALHULEU: Champerico, *Kellerman 4978* (US). SUCHITEPEQUEZ: Tiquisate, 100 m, *Steyermark 47630* (F). SOLOLA: Guatalón, 190 m, *Steyermark 48080* (F, US). SACATEPEQUEZ: Villa Nueva, foot of adobe wall, *Porter 1308* (DS, GH). GUATEMALA: La Aurora, *Aguilar G. 502* (F). ZACAPA: Gualan, waste places and yards, 620 ft, *Deam 6288* (F, GH, MICH, MO, NY, US). AMATITLAN: Río Amatitlán, 3900 ft, *J. D. Smith 1936* (GH, US). ESCUINTLA: near San José, roadside, sea level, *Standley 64062* (F, NY). SANTA ROSA: Cerro Gordo, 3500 ft, *Heyde & Lux 3958* (F, PH, US). JUTIAPA: near Jutiapa, gravelly open slope, ca. 850 m, *Standley 74980* (F).

BRITISH HONDURAS. COROZAL: Santa Rita, occupied clearing, *Lundell 4773* (ARIZ, DS, F, GH, MEXU, MICH, MO, NY, TEX). CAYO: El Cayo and vicinity, *Chanek 159* (F, MICH).

EL SALVADOR. SANTA ANA: Santa Ana, *Porter 1280* (GH, ITIC). SONSONATE: near Armenia, dry field, *Standley 23538A* (DS, US). LA LIBERTAD: La Libertad, railroad track, *Porter 1260* (DS, GH, ITIC). SAN SALVADOR: San Salvador, *Calderón 349* (GH, MO, NY, US). LA PAZ: 0.5 mi N of Comalapa toward Santo Tomás, roadside, *Porter 1286* (GH, ITIC). SAN VICENTE: near San Vicente, old corn field, *Standley 21708* (GH, US). SAN MIGUEL: Laguna de Olomega, ca. 1.8 km W of Hacienda Potrero Santo, ca. 60 m, *Tucker 892* (F, UC, US). LA UNION: La Unión, sunny fields on edge of forest, *Grant 706* (F, GH).

HONDURAS. CORTES: Finca Zapote, near La Lima, 30 m, *Williams & Molina R. 12458* (F, GH). COMAYAGUA: near Comayagua, ca. 600 m, *Standley & Chacón P. 5614* (F). MORAZAN: near Zamorano, sand along Río de la Orilla, 850 m, *Molina R. 261* (F, GH, MO, UC, US). EL PARAISO: Yascarán, open bank, 930 m, *Standley 25790* (F). CHOLUTECA: near Pespire, 160–200 m, *Standley 27259* (F).

NICARAGUA. CHINANDEGA: Corinto, *Greenman & Greenman 5828* (GH, MO). MANAGUA: Managua, railroad track, *Porter 1190* (DS, GH). MASAYA: Masaya, *Baker 211* (DS, GH, MO, NY, UC). CARAZO: near Jinotepe, dry thicket, ca. 600 m, *Standley 8536* (F). CHONTALES: near Juigalpa, roadside, ca. 160 m, *Standley 9417* (F).

COSTA RICA. GUANACASTE: Nocoya, roadsides, *Tonduz 13919* (CR, GH, US). PUNTARENAS: Puntarenas, railroad track, *Porter 1136* (CR, GC, GH, IJ). ALAJUELA: El Coyolar, dry field, ca. 240 m, *Standley 40079* (US).

PANAMA: CANAL ZONE: between Panamá and Corozál, 20–30 m, *Pittier 4443* (F, GH, NY, US).

BAHAMA ISLANDS. FORTUNE: *Hitchcock*, Nov 1890 (MO). NEW PROVIDENCE: hill S of Lyford Cay, *Degener 18742* (GH, NY, PH).

CUBA. PINAR DEL RIO: near Mariel, sandy flat ground along coast, *Palmer & Riley 711* (NY, US). HAVANA: Havana, *Schott 97* (BM). MATANZAS: near Matanzas, *Gundlach 291* (CAS). LAS VILLAS: Las Auaras, banks of Río Arimao, *Gonzales 539* (A, BM, IJ, MICH, NY). ORIENTE: Hicotea Estate, banks of Río Cañas, *Bro. Clemente 5699* (GH, US).

CAYMAN ISLANDS. GRAND CAYMAN: Bosun Bay, near Hell, pasture, coral rock and soil, 10–20 ft, *Kings GC403* (BM, MO).

JAMAICA. HANOVER: Lucea, *Hitchcock*, 9 Jan 1891 (MO). WESTMORLAND: New Hope Estate, 1.5 mi W of Little London, garden, 175 ft, *Proctor 11202* (IJ). ST. JAMES: Montpelier, *Churchill*, 16 Mar 1897 (GH). ST. ELIZABETH: Giddy Hall, *Maxwell*, Apr 1926 (BM). CLARENDON: halfway between Amity Hall and Portland Cottage, roadside at edge of sugarcane plantings. *Porter 1039* (GH). ST. CATHERINE: Spanish Town Road, 100 ft, *Campbell 6298* (BM, UCWI). ST. ANDREW: Mona, weedy field, *Crosby, Hespenheide & Anderson 69* (F, GH, MSC, UC). ST. THOMAS: Albion, *Orcutt 1421* (UC).

HAITI. NORD: Bayeux, dry streambed, sea level. *Nash 92* (F, NY). ARTIBONITE: Montagnes de Terre Neuve, 400 m, *Buch 55* (IJ). SUD: Miragoâne, roadside, *Eyerdam 32* (GH, US). OUEST: Port au Prince, 350 m, *Holdridge 1039* (F, MICH, NY, US). GONAVE: near Pikmi, cultivated and waste places, *Leonard 5194* (GH, US).

DOMINICAN REPUBLIC. MONTE CRISTI: Santiago, margins of Río Yaque, *Jiménez 1844* (US). AZUA. Azua, *Rose, Fitch & Russell 4012* (NY, US). BARAHONA: near Barahona, 20 m, *Fr. Fuertes 1574* (BM, F, GH, NY, US). PACIFICADOR: Pimental, along railroad, near sea level. *Abbott*

643 (US). SANTO DOMINGO: Santo Domingo, seashore, *von Türckheim 2547* (BM, GH, MO, NY, US). MACORIS: 20 km W of San Pedro de Macoris, limestone outcrop, *Howard & Howard 9496* (GH, NY, US).

PUERTO RICO. AGUADILLA: Camuy, *Underwood & Griggs 197* (NY, US). MAYAGUEZ: near Yauco, *Heller 6296* (CAS, F, GH, MO, NY, PH, US). ARECIBO: near Manati, cultivated area, *Sintenis 6731* (BM, F, GH, MO, NY, US). PONCE: Cayo Muertos, waste grounds, *Britton, Cowell & Brown 4985* (F, MO, NY, US). SAN JUAN: Cataño, waste ground, *Heller & Heller 114* (F, NY, US). GUAYAMA: Guayama, *Kuntze 578* (NY). HUMACAO: Luquillo Beach, along sidewalk, *Howard & Nevling 15523* (A). VIEQUES ISLAND: Isabel Segunda to Cerra Encanta, roadside bank, *Shafer 2519* (NY, US). CULEBRA ISLAND: Culebra, waste places, *Britton & Wheeler 282* (F, NY, US).

VIRGIN ISLANDS. ST. THOMAS: *Eggers 8* (F, NY). TORTOLA: Experiment Station, waste places, *Fishlock 131* (NY, PH). ST. CROIX: roadside, *Ricksecker 138* (F, GH, MO, NY, UC, US).

LEEWARD ISLANDS. ANGUILLA: near Blowing Point, roadside, *Proctor 18685* (BM, IJ). ST. BARTHELEMY: Gustavia, 2 m, *Questel 193* (US). ST. EUSTATIUS: Orangestäd, along roads, *Stoffers 3905* (A). ST. KITTS: near Basseterre, roadside, *Britton & Cowell 137* (NY, US). ANTIGUA: Cedar Valley, cultivated lands in drier districts, *Box 871* (GH). GUADELOUPE: Basse-Terre, *Fr. Duss 2427* (US). DESERADE: Grand Anse, roadside, 1 m, *Proctor 21294* (IJ). DOMINICA: Grand Savannah, grassy coastal xerophytic shallow-soiled areas, *Hodge & Hodge 3762* (GH, US).

WINDWARD ISLANDS. MARTINIQUE: St. Pierre, *Hahn 987* (BM, PH). ST. VINCENT: sandy land or cultivated fields, *Smith & Smith 584* (GH). BARBADOS: near Combermere School, *Dash 224* (F, NY, US). GRENADA: St. George's, ditch, *Broadway,* 2 Apr 1905 (NY).

COLOMBIA. ATLANTICO: Cabica, island in Río Magdalena, *Bro. Elias 1218* (F). MAGDALENA: Santa Marta, 250 ft, *H. H. Smith 572* (MICH, TEX, UC, WIS). BOLIVAR: near Cartagena, ca. sea level, *Killip & Smith 14039* (COL, F, GH, NY, US). CORDOBA: Montería, riverbank, 20–50 m, *Pennell 4706* (F, GH, MO, NY, US).

VENEZUELA. ZULIA: Maracaibo, *s. coll.* (CAS). TRUJILLO: La Concepción, 2500 ft, *Reed 1005* (MICH). DISTRITO FEDERAL: Blandin, waste places, *Pittier 11618* (NY, US). ANZOATEGUI: Guanta, roadside, ca. sea level, *Potter 5149* (US). BOLIVAR: Ciudad Bolívar, near river, ca. 35 m, *Holt & Gehriger 33* (US).

A specimen of *Kallstroemia maxima* at CAS, purportedly collected in California and labeled "*Jesse D. Skoss,* 7 May 1948. Kern Co.: Kern River Canyon, 7 miles below Hobo Hot Springs.", actually seems to have been collected by A. S. Crafts in the Dominican Republic (Dr. John M. Tucker, personal communication). There is also a specimen of *Tribulus cistoides* at CAS bearing Skoss' name and the same locality data. I have indicated previously (Porter, 1963) that this latter collection was made in California, but it, too, apparently was collected in the Dominican Republic by Crafts.

COMMON NAMES. Many common names have been applied to *Kallstroemia maxima.* This is to be expected with a plant that is so frequent and widespread among peoples who often utilize their natural flora and its products. The names reported in the litera-

ture, or noted on herbarium labels, are Abrojo (Cuba, Nicaragua, Puerto Rico); Chax-chauxnuc (Quintana Roo, Mexico); Cresson Courant (Guadeloupe); Golondrina, Guía de Parra, Hierba de Parra (El Salvador); Hierba de Pasmo (Venezuela); Hierba de Pollo (Colombia, El Salvador, Panama); Maconcherie (Dominica); Mata (Costa Rica); Pale-flowered Turkey-blossom (Jamaica); Parsley (Grand Cayman); Patagon (Martinique); Police Macca (Jamaica); Pourpier Bâtard (Guadeloupe); Pourpier Courant, Pourpier Rampant (Martinique); Shanapmucui (British Honduras); Talcacao (Costa Rica); Taraya (El Salvador); Verdolaga (Costa Rica, El Salvador, Venezuela); Verdolaga Blanca, Verdolaga del Caballo, Verdolaga del Monte, Verdolaguita (El Salvador); Xichiak (Quintana Roo); Xichilak (Yucatan, Mexico); Yerba de Gallina (Honduras); and Yerba de Paloma (Guerrero, Mexico).

The prevalence of Verdolaga or its derivatives as a common name for this species throughout much of Latin America is explained by its resemblance to the Verdolaga Vera (true verdolaga), *Portulaca oleracea* L. *(Portulacaceae)*. The latter is another weedy plant common to the same area as *Kallstroemia maxima*, superficially similar to it, and much used by the native populations as a potherb.

It should be noted that the name *Caltrop* is often given to various members of the genus in manuals and floras, but it is to be doubted that anyone but a botanist would apply this common name to a *Kallstroemia*. It is more aptly applied to the spiny-fruited species of *Tribulus*, which show a decided resemblance to their namesake, a medieval weapon used to impede charging cavalry.

TAXONOMY. The name *Kallstroemia canescens* has been applied to specimens of *K. maxima* from southwestern Mexico with strigose fruits. Whereas the fruits of *K. maxima* usually are glabrous, individuals with strigose fruits are found occasionally. They come from scattered places throughout the range of the species, and taxonomic recognition on the basis of this single character is not warranted.

VARIATION. In *Kallstroemia maxima* there is a noticeable amount of variation in stem color, in flower size and color, in anther and pollen color, and in peduncle length and the amount of peduncle curvature at fruiting time. Variation is particularly striking in this

species because these morphological characters may vary within the local population. Other species of the genus may be equally variable with respect to the same characteristics, but the variation occurs between populations, apparently never within them.

This interpopulation variation is especially common in Central America. In Costa Rica, for instance, where *Kallstroemia maxima* was observed in the town of Puntarenas the populations consisted of two morphological types. One type had yellow-orange flowers 1–1½ cm in diameter with yellow anthers and pollen, the sepals were about two-thirds as long as the petals, and the peduncles were 2–2½ cm long, bent strongly at the base and straight above. The second type had pale yellowish-white flowers 7–8 mm in diameter with red anthers and pollen; the sepals were as long as the petals, and the peduncles were 6–14 mm long and curved through their entire length. An accurate count of the two types in the populations was not taken, but they were estimated to be present in approximately equal numbers. Intermediates were not seen. Progeny of collections of both types *(Porter 1135, 1136)* proved to be self-compatible when grown in the greenhouse.

The situation discussed above in *Kallstroemia maxima* is similar to that described by Lewis (1963) for *Gayophytum* "taxon *B*" *(Onagraceae)*. Discontinuous phenotypic variation in populations of the latter autogamous taxon could have a simple genetic basis, and if so such differences do not warrant formal taxonomic recognition. The same conclusion is applicable in this instance to *K. maxima*, especially in light of the populations reviewed below, although data concerning cytology and breeding behavior (i.e., the extent of outcrossing) are lacking.

Populations of *Kallstroemia maxima* examined in Managua, Nicaragua, and Ilopango and San Salvador, El Salvador, displayed all combinations of flower size and color, as well as anther and pollen color found in the two Puntarenas types. Stem color here varied independently as well, being either yellow-green or reddish. In one Managua population, some plants were also prostrate with smaller leaves, and the others were decumbent with larger leaves, additional characters that appeared to vary independently. This same population yielded individuals with yellow anthers and pollen and with flowers which had a few red pollen grains on their stigmas. Others possessed flowers with red anthers and pollen, and with a few yellow grains on their stigmas. This information

suggests that these characters are under simple genetic control. Further evidence in support of this conclusion, at least for anther and pollen color, is provided by greenhouse plantings of the progeny of *Porter 1489,* an individual of *K. maxima* from Mazatlán, Sinaloa, with red-orange anthers and pollen. Some of the progeny plants had red-orange anthers and pollen, as in the parent, others had yellow anthers and pollen.

Another variation in flower color in this species is found in some populations in Guerrero and Michoacán. Here, the petals are proximally cream with a red spot at the base. Specimens with this red spot also have red anthers and pollen.

As mentioned above, there is some variation in this species with respect to fruit pubescence. Classically, the presence of a glabrous fruit has been used as the key character for the recognition of *Kallstroemia maxima.* This is true for the majority of individuals, but there are exceptions. Specimens with a varying pattern of strigose fruit pubescence have been found at scattered localities throughout the range of the species, some fruits being strigose only at the base, but others across the abaxial surfaces of the mericarps to the base of the style. The only area where the fruit pubescence presents a more consistent pattern is in southwestern Mexico where *K. maxima* overlaps with *K. rosei.* The sepals of individuals of *K. maxima* in this region also vary toward those of *K. rosei.* They extend further beyond the mature mericarps and the margins are more involute than is true for specimens from other parts of the species range. This variation possibly is due to the introgression of genes from *K. rosei.*

Despite the great range of variation in certain morphological characters in *Kallstroemia maxima,* it appears best not to give formal taxonomic recognition to the variants. The evidence indicates that they have a simple genetic basis, and there are no established ecological or geographical correlations present. More information, particularly of a cytogenetical nature, may lead to a more precise interpretation of the variability present.

RELATIONSHIPS. This species is most closely related to *Kallstroemia pubescens* and *K. rosei.* A discussion of the three species will be found above.

Millspaugh (1916, p. 428), in a discussion of *Tribulus alacranensis,* a species supposedly endemic to the Alacran Shoals off the northern coast of Yucatán, Mexico, wrote of its "probable

parent *T. maximus* [= *Kallstroemia maxima*]." This undoubtedly was a slip of the pen, as he earlier (Millspaugh, 1900) indicated *T. alacranensis* as being a close relative of *T. cistoides*. It is probably conspecific with the latter, although a recent survey of the flora of these small islands (Bonet & Rzedowski, 1962) recognized *T. alacranensis* as a distinct species. However, *T. alacranensis* has no closer affinities to *Kallstroemia* than does any other species of *Tribulus*.

Kallstroemia maxima × K. pubescens?

As has been indicated in the introductory material, under "Hybridization," there are a number of collections of the genus from Colombia and Venezuela which appear to be morphologically intermediate between *Kallstroemia maxima* and *K. pubescens (Map 2)*. Comparative morphology suggests that these specimens may be the result of hybridization between the species indicated above, but there is no genetical evidence that this is the case. Until this becomes available, either through further field studies or crossing experiments, it is thought best to consider these specimens only as putative hybrids.

SPECIMENS EXAMINED. COLOMBIA. LOCALITY UNKNOWN: Magdalena, 600 m, *Triana*, 1851–1857 (BM). ATLANTICO: Barranquilla, *Bro. Paul B35* (US); around Galapa and Baranoa, *Dugand & Jaramillo 3271* (COL, US); wet ground at edge of marsh, Malambo, *Porter 1118* (GH); corral, Ponedera, *Porter 1123* (GH). BOLIVAR: near Cartagena, *Bro. Heriberto 1* (US). CORDOBA: highway from Ceratí to Sahagún, 120 m, *Garcia Barriga 13445* (COL, US); dry rich soil near Montería, ca. 20 m, *Araque Molina & Barkley 19B01168* (COL, US). ANTIOQUIA: scattered woods on outskirts of Dabeiba and right bank of Río Sucio, ca. 1350 m, *Gutierrez V. & Barkley 17C486* (CAS, COL, GH); humid forest below Santa Elena summit, Medillín-Río Negro road, ca. 2500 m, *Barva L., Araque M. & Saiz A. 448* (US). VALLE: moist field, Dagua, *Killip 5432* (GH, NY, PH, US); San Jerónimo, 980 m, *Cuatrecasas 22807* (F, US). CUNDINAMARCA: near Anapoima, 600 m, *Triana 3744* (NY, US); Girardot, *Pérez Arbeláez 426* (COL, US), *Toro 56* (COL, NY); Tocaima, *Pérez Arbeláez 2442* (COL, US). HUILA: talus at base of dry eroded river bluffs, Río Ambicá just above confluence with Río Cabrera, *Fosberg 19334* (COL, US).

VENEZUELA. TRUJILLO: La Concepción, 2500 ft, *Reed 1005* in part (US).

2. **Kallstroemia rosei** Rydb. in Vail & Rydb., N. Amer. Fl. **25**:113. 1910

TYPE: Mexico, Morelos: near Yautepec, 27 August 1903, *J. N. Rose & Jos. H. Painter 6562* (US, holotype; NY, isotype).

Annual (occasionally perennial?); *stems* prostrate to decumbent, to 1 m long, densely hirsute and sericeous with white or gray apically-directed trichomes; *stipules* 4–9 mm long, ca. 1.5 mm wide; *leaves* obovate, 2–5 cm long, 1.5–5 cm wide; *leaflets* (2–)3(–4) pairs, ovate or oblong, appressed-hirsute, veins and margins sericeous, 12–26 mm long, 6–17 mm wide, terminal pair largest; *peduncles* usually shorter than leaves, thickened distally, 2–5 cm long, more or less curved in fruit; *flowers* pentamerous, 2–3.5 cm in diameter; *sepals* narrowly ovate, 6–10 mm long, 2–3 mm wide, hirsute and strigose, longer than style in flower, in fruit shorter than beak and usually spreading from base of fruit and curving upward, margins becoming sharply involute, persistent; *petals* white to light orange, base green to white or yellow, drying white, obovate, 5–17 mm long, 5–20 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid, rarely linear, ca. 1 mm in diameter, they and pollen red-orange, rarely yellow; *ovary* conical, 1–2 mm high, strigose; *style* 2–3 mm long, conical, base hirsute; *stigma* capitate, obscurely 10-lobed, ca. 1 mm long, papillose; *fruit* ovoid, 5–6 mm in diameter, strigose; *beak* 4–10 mm long, ca. twice as long as fruit body, cylindrical, base somewhat conical and hirsute; *mericarps* 4 mm high, abaxially tubercled and cross-ridged, sides slightly pitted, adaxial edge angled. *Fig. 2a, 2b. Map.* 3.

FLOWERING DATES. Mainly from June through September, following the summer rains, but occasionally flowering until March.

DISTRIBUTION AND HABITAT. Disturbed areas in the pine-oak forests of the mountains of northeastern, central, and southern Mexico, and occasionally spreading to lower elevations *(Map* 3). Found from 200 to 3150 m, mainly above about 1000 m. Sympatric with *Kallstroemia parviflora* to the north and *K. maxima* to the southwest, and slightly overlapping with *K. californica, K. grandiflora, K. hirsutissima,* and *K. pubescens* in parts of its range.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia rosei* may be recognized by the combination of its obovate leaves, usually three pairs of leaflets, flowers 2–3½ cm in diameter, hirsute and strigose sepals which spread from the base of the mature fruit and curve upward, sharply involute sepal margins making the sepals appear linear or linear-lanceolate, usually white petals, usually red-orange anthers and pollen, conical ovary, strigose fruit, ring of white hirsute pubescence at the base of the beak, the latter being about twice as long as the fruit body, and a capitate obscurely ten-lobed stigma. The only other species from the same area with which it is likely to be confused is *Kallstroemia maxima.* The latter is easily distinguished from *K. rosei* by its flowers of from 7–25 mm in diameter, hirsute sepals which clasp the base of the mature fruit, only their scarious margins becoming involute, and usually glabrous ovaries and fruits. In those rare individuals of *K. maxima* with pubescent ovaries and fruits, these organs are sparingly

strigose. *Kallstroemia maxima* tends also to be smaller in overall plant size and less decumbent than *K. rosei*. In areas where the two overlap in distribution, petal color is white in *K. rosei* and yellow to orange in *K. maxima*.

REPRESENTATIVE SPECIMENS EXAMINED. MEXICO. DURANGO: Trancas Canyon, ca. 7 mi SW of Chocolate, among limestone boulders, 1350 m, *Correll & Johnston 20014* (LL). NUEVO LEON: Cerro del Obispado, along road, 1500 ft, *Lacás 36* (F); Monterrey, 1800 ft, *Fisher 41* in part (CAS, DS, F). TAMAULIPAS: 5 km S of Hoja Verde, up arroyo, *Stanford, Lauber & Taylor 2219* (DS, GH, MO, NY, RSA, US); 4 mi S Jaumave, ditch bank, *Stanford, Lauber & Taylor 2283* (GH, NY, US); mountain top 7 km SW of Miquihuana, forest floor of low vegetation in forest of large pines, 3150 m, *Stanford, Retherford & Northcraft 917* (ARIZ, DS, GH, MO, NY). SAN LUIS POTOSI: 10 km S of Cárdenas, trailside, 1100 m, *Rzedowski 4588* (TEX); Río Verde, *Palmer 3* (F, GH, MO, NY, US). AGUASCALIENTES: 43 km W of Aguascalientes, gentle S slope in xeric matorral, 2045 m, *Detling 8737* (MICH); 9 mi E of Aguascalientes toward Ojuelos, brush-covered hills, 2000 m, *McVaugh 16627* (MICH). JALISCO: Jaday, *Davis*, 6 July 1959 (TEX); La Palma, *M. E. Jones 109* (MO, MSC, POM, US). GUANAJUATO: Cortazar, *Knobloch 1081, 1082* (MICH, MSC); near Irapuato, barren land, *Kenoyer 1859* (GH). QUERETARO: near San Juan del Río, stony hillside, *Rose, Painter & Rose 9617* (US). HIDALGO: Jacala, wooded mountain ravine, 4500 ft, *Chase 7200* (F); Zimapán, *Coulter 780* in part (GH, NY, PH). MICHOACAN: ca. 7 mi N of Ciudad Altamirano, *Porter 1373* (DS, GH. MEXU); Coalcomán, llano, 1000 m, *Hinton 13981* (GH, LL, NY. PH, US); Zitácuaro to San José Purua, trailside, lush shrubbery, *Hinton 13050* (ARIZ, GH, LL, MICH, NY, TEX, US). MORELOS: Km 117 on Cuernavaca-Taxco highway, *Langman 2081* (MEXU, PH); 5 km NW of Zacatepec toward Cuautla, edge of highway in sugarcane plantation, *Porter 1443* (GH, MEXU). PUEBLA: 1 mi E of Puebla-Morelos border between Axochiapan and Atencingo, fine sandy fill at roadside, *Porter 1457* (DS, GH, MEXU); 5 mi NW of Tehuacán toward Puebla, edge of highway, *Porter 1447, 1449, 1450* (GH). GUERRERO: Cutzamala, dry hill, *Hinton 5789* (GH, LL, NY, PH, US); 10 mi W of Iguala toward Teloloapan, roadside, *Porter 1345* (DS, GH, MEXU); Río Balsas, *Orcutt 4169* (BM, F, GH, MO, US). OAXACA: Cuicatlán, 1900 ft, *L. C. Smith 494* (GH); near Oaxaca, 1550 m, *Conzatti 1832* (F, GH, MEXU). CHIAPAS: Tuxtla Gutiérrez, vacant lot, 1800 ft, *Breedlove 10619* (DS, GH).

VARIATION. Fruit pubescence in *Kallstroemia rosei* varies from dense to sparse. Lightly pubescent fruits appear most commonly in the area south of the volcanic cordillera of south-central Mexico where this species is sympatric with *K. maxima*. This variation in fruit pubescence may be due to the introgression of genes from *K. maxima*. There is also some evidence that older fruits tend to be less pubescent than younger ones because of the loss of trichomes.

RELATIONSHIPS. *Kallstroemia rosei* is most closely related to *K. maxima*. A discussion of their differences will be found above.

3. **Kallstroemia pubescens** (G. Don) Dandy in Keay, Kew Bull. **10**:138. 1955

Tribulus pubescens G. Don, Gen. Syst. 1:769. 1831. TYPE: Cape Coast [Accra, Ghana], *G. Don s. n.* (BM, holotype, not seen).

Kallstroemia minor Hook. f. in Hook., Niger Fl. 269. 1849. *nom. superfl.* Based on *Tribulus pubescens* G. Don, cited as a synonym.

Tribulus maximus var. *minor* Oliver. Fl. Trop. Afr. 1:284. 1868. TYPE: Cape Coast, *T. Vogel.*

Kallstroemia caribaea Rydb. in Vail & Rydb., N. Amer. Fl. **25**:111. 1910. TYPE: West Indies, Montserrat: Cocoanut Hill, creeping in cotton patch, fls. yellow; 5 February 1907, *J. A. Shafer* 388 (NY, holotype; F, US, isotypes). The name "*Kallstroemia maxima* var. *caribaea* (Rydb. in Vail & Rydb.) Macbr." occasionally has been applied to this taxon. However, this combination was never validated. Macbride (1930) argued that the taxon merited only varietal recognition but did not make the relevant combination.

Kallstroemia glabrata Rydb. in Vail & Rydb., *op. cit.* 112. 1910. TYPE: Mexico, Guerrero: Acapulco and vicinity, October, 1894, to March, 1895 [November, 1894, according to McVaugh (1956)], *Edward Palmer 131* (US, holotype; GH, isotype).

Kallstroemia longipes Rydb. in Vail & Rydb., *op. cit.* 114. 1910. TYPE: Mexico, Sinaloa: Rosario; 22 July 1897, *J. N. Rose 1829* (NY, holotype; MEXU, MO, US, isotypes).

Annual; *stems* prostrate to decumbent, to 1 m or more long, sparsely to densely hirsute and sericeous with apically-directed or rarely retrorse fine white trichomes; *stipules* 2-6 mm long, 1–2 mm wide; *leaves* obovate, 1–6 cm long, 1.5-5 cm wide; *leaflets* (2–)3(–4) pairs, elliptical to obovate, appressed-hirsute to glabrate, veins and margins more or less sericeous, 3–26 mm long, 5–17 mm wide, terminal pair largest; *peduncles* shorter than or equaling subtending leaves, 1–3.5 cm long, length and amount of curvature in fruit variable; *flowers* pentamerous, 9–15 mm in diameter; *sepals* lanceolate, 4–8 mm long, 2–3 mm wide, hispidulous with fine white trichomes of two lengths, in flower ca. as long as style, spreading from base of mature fruit and appearing linear-lanceolate through margins becoming sharply involute, persistent; *petals* white through yellow to pale orange, base green, fading white or yellow, obovate, 6–11 mm long, 5–8 mm wide, marcescent; *stamens* as long as style; *anthers* globose, less than 1 mm in diameter, they and pollen yellow or red-orange; *ovary* pyramidal, 3–5 mm long including style, densely appressed short-pilose with fine white trichomes; *style* stout, conical, rarely cylindrical above; *stigma* capitate, obscurely 10-lobed, ca. 1 mm long, papillose; *fruit* ovoid, 5–6 mm in diameter, densely appressed short-pilose; *beak* 5–8 mm long, ca. as long as fruit body, short-pilose to glabrous, cylindrical, base conical; *mericarps* 3–4 mm high, ca. 1 mm wide, abaxially cross-ridged and tubercled to rugose, sides pitted, adaxial edge angled. *Fig. 3, 3b. Maps 4, 5.*

FLOWERING DATES. Apparently flowering throughout the year whenever sufficient moisture is available for seed germination and plant growth.

DISTRIBUTION AND HABITAT. The Lesser Antilles, Puerto Rico, and Jamaica; across northern South America and north through Central America to Yucatán on the east and Sinaloa on the west

coast of Mexico; south through Colombia and Ecuador to northern Peru *(Maps 4 and 5)*. Introduced into Florida, Ghana and Nigeria, Africa (Keay, 1955), and West Bengal, India (Bennet, 1965). Disturbed areas from sea level to 1400 m, most common at lower elevations. Sympatric with *Kallstroemia hintonii* and *K. standleyi*, and over most of its range with *K. maxima*. Extending into the ranges of *K. curta* in the Caribbean and *K. californica*, *K. grandiflora*, and *K. rosei* in western Mexico.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia pubescens* may be recognized by its combination of obovate leaves, usually three pairs of leaflets, usually white flowers 9–15 mm in diameter, hispidulous sepals spreading from the base of the mature fruit, the sepals appearing linear or linear-lanceolate through the sepal margins becoming sharply involute, usually red-orange anthers and pollen, pyramidal ovary, densely appressed short-pilose fruit, with the beak about as long as the fruit body, and a capitate obscurely ten-lobed stigma. *Kallstroemia maxima* is the only species from the same area with which *K. pubescens* is likely to be confused. The two are readily distinguishable to the naked eye because of fruit and sepal differences. In *K. maxima*, the sepals are hirsute, clasp the mature mericarps, and only their scarious margins become involute; the fruit is usually glabrous, rarely being strigose. In localities where the two species grow together, the herbage of *K. pubescens* tends to be lighter in color and less succulent than that of *K. maxima*. In such areas, the petals of *K. pubescens* invariably are white, while those of *K. maxima* are yellow to orange.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. FLORIDA. Franklin Co.: Apalachicola, *Chapman s. n.* (MO), *4099* (NY).

MEXICO. SINALOA: Rosario, *Rose 1830* in part (NY). NAYARIT: near Jesús María, dry woodland, *Feddema 1329* (MICH). JALISCO: Bolaños, *Rose 3693* in part (NY). MICHOACAN: El Capire, 15 mi SSW of Apatzingán, moist open, often by standing water, *Leavenworth 439* (ARIZ, F, GH, MICH, MO, NY); Tepalcatepec, grassy hill, 350 m, *Hinton 12097* (DS, GH, MICH, NY, US). GUERRERO: Atoyac, shrubby plain, *Hinton 14543* (ARIZ, GH, LL, NY, PH, US); Placeres to Pinzon Morado, llano, 400 m, *Hinton 9119* (ARIZ, GH, LL, NY, US). OAXACA: Puerto Angel, *Orcutt 5017, 5029* (DS); 4 km NNE of Tehuantepec, gravelly roadside, flat grazed areas, *King 1315* (MICH, NY, SMU, TEX, UC, US). CHIAPAS: 8 mi E of Cintalapa on Highway 190, wooded slope, 2200 ft, *Breedlove 10315* (DS, GH). YUCATAN: Valladolid, *Steere 1693* (F, MEXU, MICH). QUINTANA ROO: Chichankanab, *Gaumer 1570* in part (BM, MO).

GUATEMALA. ZACAPA: near Zacapa, damp field, ca. 200 m, *Standley 73599* (F, US).

EL SALVADOR. LA PAZ: Bosque la Herradura, 100 m, *Lagos*, 28 Sept 1956 (ITIC).

HONDURAS. SANTA BARBARA: San Pedro Sula, 1000 ft, *Thieme 5170* (F, GH, US). COMAYAGUA: W of Comayagua near El Taladro, savannahs and roadside, 650 m, *Molina R. 14287* (F). VALLE: San Lorenzo, 20 m, *Valerio Rodriguez 3449* (F).

NICARAGUA. CHINANDEGA: E base of Volcán Cosegüina, *Howell 10269* (CAS). MATAGALPA: just N of Las Maduras, rocky roadside embankment, *Porter 1215* (GH). MANAGUA: E of Tipitapa toward Rama at Km 43, edge of highway, *Porter 1213* (DS, GH, IJ). MASAYA: Masaya, *Baker 211* (ARIZ, POM), *665* (US). CHONTALES: near Juigalpa, waste ground, ca. 160 m, *Standley 9316* (F).

COSTA RICA. GUANACASTE: Catalina, forest, *Stork 2769* (F, MICH). PUNTARENAS: Mata de Limón, along railroad track, 7 m, *Porter 1187* (CR, GH).

PANAMA. PANAMA: near beach at Nueva Gorgona, *Duke 4499* (MO).

JAMAICA. ST. ANDREW: St. Benedict's School, E of Harbour View, bank, ca. 25 ft, *Porter 1034* (GH, IJ, UCWI).

PUERTO RICO. GUAYAMA: near Salinas, sandy plain, *Britton, Britton & Brown 6045* (NY).

VIRGIN ISLANDS. ST. THOMAS: along road, *Eggers*, June 1887 (US). TORTOLA: Experiment Station, waste places, *Fishlock 131A* (NY).

LEEWARD ISLANDS. ST. BARTHELEMY: Gustavia. *Questel 164, 201* (NY). SABA: *Boldingh 1951B* (NY). ST. EUSTATIUS: Oranjestad to Ft. de Windt, along road, *Stoffers 3500* (IJ). ST. KITTS: *Walsh*, Sept 1889 (NY). ANTIGUA: Cedar Valley, cultivated lands in drier districts, *Box 871* (BM, US). MONTSERRAT: O'Garras estate, S of Plymouth, track to cove, *Proctor 19029* (BM, IJ). GUADELOUPE: Viux Habitants, 10 m, *Questel 2167* (US).

WINDWARD ISLANDS. MARTINIQUE: Morne Vert, dry thicket, 350 m, *Stehlé & Stehlé 4784* (US). ST. VINCENT: sandy soil near seashore, *Smith & Smith 388* (UCWI). BARBADOS: Hastings, neglected gardens, *Waby 2* (F, US). BEQUIA: open lands and clearings, *Joseph B241* (NY). CANOUAN: sandy beach trail, *Howard 11096* (BM, IJ, NY). GRENADA: St. George's, *Broadway*, 16 Aug 1905 (F, GH).

TOBAGO: Stoer Bay direction, open land, *Broadway 9065* (A, BM, MO).

CURAÇAO: Groot St. Martha, sea level, *Fr. Arnoldo 2116* (US).

COLOMBIA. BOLIVAR: near Cartagena, *Bro. Heriberto 1, 72, 301* (US). ATLANTICO: Salgar, roadside, *Porter 1111* (COL, DS, GH, IJ). MAGDALENA: Santa Marta, 250 ft, *H. H. Smith 572* (BM, COL, F, GH, MICH, MO, NY, PH, TEX, UC, US, WIS). GUAJIRA: *s. coll. 596* (US). BOYACA: Puerto Boyacá, *Romero Castañeda 3062* (COL). CUNDINAMARCA: Arbeláez, 1400 m, *Garcia Barriga 4878* (COL, US). TOLIMA: Armero, *Barreneche E. 9* (COL).

VENEZUELA. ANZOATEGUI: Guanta, roadside, ca. sea level, *Potter 5149* (GH, US). NUEVA ESPARTA: El Valle, Margarita I., *Miller & Johnston 7* (ARIZ, BM, F, GH, MO, NY, POM, US).

ECUADOR. MANABI: Bahía, *Mille 1140, 1994* (F). GUAYAS: Playas, sandy seashore, *Asplund 5063* (CAS, F, NY, US). LOJA: Río Guayabas 5 km NW of Catamayo, dry brushy thorn-forest flats, 1300 m, *Fosberg & Giler 22937* (COL, US).

PERU. PIURA: Pariñas Valley, *Haught F-51* (F), *147* (F, GH, NY, PH, US).

GHANA: Accra, near beach, *Enti*, 31 May 1964 (GH).

Two specimens of *Kallstroemia pubescens* have been seen that were supposedly collected in the southwestern United States. These are "*Walter H. Evans*, 23 June 1891, Ft. Hancock, Texas" (MO) and "*Dr. Woodhouse*, 29 Sept. 1851. N. M. Camp No. 6, Little Colorado" (PH), the latter from Apache County, Arizona. These collections are sufficiently removed from the known range of the species, which is essentially tropical, to cast doubt on the authenticity of the label data. The problem of the wrong label being applied to a specimen also has been encountered in *K. grandiflora* and *K. maxima*.

A mixed collection of *Kallstroemia pubescens* and *K. maxima* from Georgia, *Beyrich s. n.* (MO), probably is a product of a misapplied or lost label. A collection of this species from Florida, *Chapman s. n.* (MO), is labeled "Cult."

COMMON NAMES. Most of the common names applied to *Kallstroemia pubescens* are identical to those used in the same area to designate the superficially very similar *K. maxima*. Common names of which I am aware are Abrojo (Colombia); Angglo Boobo (Bonaire, Curaçao); Anglo Bobo (Aruba, Bonaire, Curaçao); Coclí (Colombia); Golondrina (Costa Rica); Huistolohuetzli (Guerrero, Mexico); Pourpier Bâtard (Guadeloupe, Martinique); Pourpier Jaune Courant (Martinique); Pourpier Marron (Guadeloupe); Verdolaga (Colombia, El Salvador); and Verdolaguilla (Nayarit, Mexico). In addition, Irvine (1930, p. 419) reports that in Ghana the plant is called Akwamfãnu, and that "the vernacular name comes from 'Okwan afãnu,' which means 'on both sides of the road,' probably because it is a common weed along bush paths."

TAXONOMY. The name *Kallstroemia longipes* has been given to somewhat larger than average specimens of *K. pubescens* from southwestern Mexico. However, specimens at this extreme in variation are found scattered throughout the range of *K. pubescens* and probably are due to optimum growth conditions.

As has been indicated above, this species was first described from Africa, 80 years before being recognized as distinct from *K. maxima* in the West Indies, where it is indigenous. It undoubtedly was introduced into West Africa very early, as is attested by its wide use in the native *materia medica* (cf., Irvine, 1930). Introduction probably came about through the activities of the slave

trade between West Africa and the West Indies, which began in the first half of the sixteenth century (Penrose, 1952).

VARIATION. This species is rather constant in its morphological characters, especially for one of such a wide geographical range, except for the quantitative variation in size mentioned above. Almost all specimens seen had stem trichomes that were antrorse, but in *Haught F-161* (F) and *Haught 262* (NY) from Peru, these trichomes were retrorse, similar to those in *K. peninsularis*. The anther and pollen color in most populations is red, but populations in which it is yellow occasionally are found.

RELATIONSHIPS. *Kallstroemia pubescens* is most closely related on the one hand to *K. maxima*, and on the other to the southern South American *K. tucumanensis*. Morphological comparison of *K. maxima* and *K. pubescens* will be found above.

The initial recognition of the close relationship between *Kallstroemia pubescens* and *K. tucumanensis* was by Svenson (1946b), who considered that specimens of the former from Ecuador and Peru were conspecific with those of the latter from Argentina. However, *K. tucumanensis* may be easily distinguished from *K. pubescens* by its usually two to three pairs of leaflets, pale yellow to yellow-orange flowers 4–8 mm in diameter, yellow anthers and pollen, ovoid ovary, strigose fruit, and capitate ten-ridged stigma.

4. **Kallstroemia tucumanensis** Desc., O'Don. & Lourt., Lilloa 4:218. 1939

TYPE: Argentina, Tucumán: Tapia to Vipos, elev. 750 m; 4 February 1939, *C. A. O'Donell & A. Lourteig s. n.* (LIL, holotype, not seen; DS, F, GH, NY, UC, isotypes).

Annual; *stems* prostrate to decumbent, 1–6 dm long, hirsute and sericeous with apically-directed white trichomes; *stipules* 2.5–3 mm long, ca. 1 mm wide; *leaves* obovate, 3–5.5 cm long, 1.5–3 cm wide; *leaflets* 2–3(–4) pairs, oblong, appressed-hirsute, veins and margins sericeous, 7–19 mm long, 5–11 mm wide, ultimate pair usually largest; *peduncles* shorter than subtending leaves, scarcely thickened distally, 5–6 mm long in flower, 12–20 mm long and straight or curved in fruit; *flowers* pentamerous, 4–8 mm in diameter; *sepals* subulate, 4–5 mm long, 1–2 mm wide, ca. as long as petals, hispidulous with fine white trichomes of two lengths, longer than style in flower, spreading from base of mature fruit and little longer than mericarps, margins becoming sharply involute, persistent; *petals* pale yellow to yellow-orange, narrowly obovate, 3–5 mm long, 2–3 mm wide, marcescent; *stamens* as long or longer than style; *anthers* globose, less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, ca. 1.5 mm in diameter, pubescent; *style* 1 mm long, stout, conical, strigose; *stigma* capitate, 10-ridged, less than 1 mm

long, papillose; *fruit* ovoid, 5 mm in diameter, strigose; *beak* 2–3.5 mm long, stout, conical, strigose to stigma base; *mericarps* ca. 4 mm high and 1 mm wide, abaxially more or less tubercled and laterally grooved, sides pitted, adaxial edge angled. *Fig. 4a, 4b. Map 6.*

FLOWERING DATES. November through April following summer rains.

DISTRIBUTION AND HABITAT. Semiarid southern Bolivia and northwestern Argentina *(Map 6)*. Disturbed areas, sandy riverbanks, railroad embankments, and roadsides from 420 to 1250 m. Sympatric over much of its range with *Kallstroemia tribuloides*.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia tucumanensis* is easily recognized by its combination of obovate leaves, usually two to three pairs of leaflets, pale yellow to yellow-orange flowers 4–8 mm in diameter, hispidulous sepals spreading from the base of the mature fruit and appearing linear or linear-lanceolate through the margins becoming sharply involute, yellow anthers and pollen, ovoid ovary, capitate ten-ridged stigma, and strigose fruit with a stout conical beak shorter than the fruit body. *Kallstroemia tribuloides*, the only other species in the genus known from the same area as *K. tucumanensis*, is not likely to be confused with the latter. It differs in having elliptical leaves, three to six pairs of leaflets, orange flowers 1½–2½ cm in diameter, hirsute and strigose sepals clasping and almost entirely covering the mature mericarps, sepal margins not becoming involute, orange anthers and pollen, a conical ovary, an oblong ten-ridged stigma, and a glabrous fruit with a cylindrical beak as long or longer than the fruit body.

SPECIMENS EXAMINED. BOLIVIA. SANTA CRUZ: Cabezas, 420 m, *Peredo 250* (A). TARIJA: Villamontes, *Pflanz 4041* (US).

ARGENTINA. JUJUY: Perico, roadsides, *Parodi 9070* (GH). SALTA: La Viña *Spegazzini 10025* (NY); Tiro Federal *Correa 19* (GH, NY). CHACO: La Fidelidad, *Jorgensen 1989* (GH, MO, US). TUCUMAN: Cerro del Campo, dry hard clay soil, 900 m, *Venturi 7710* (BM, CAS, GH, MO, US); La Madrid, 430 m, *Bailetti 342* (F, GH); Tapia, 700 m, *Rodriguez 223* (F, GH), railroad embankments, 750 m, *Venturi 1077* in part (GH, US); Vipos, 786 m, *Schreiter*, 24 Jan 1926, in part (A, UC). CATAMARCA: Balcozna, sandy riverbank, 1250 m, *Venturi 7142* (CAS); Campo del Pilciao, *Schickendantz 168* in part (F, UC, US). SANTIAGO DEL ESTERO: La Banda, *Lillo 6175* (F, GH); La Dársena, *Meyer 12718* (MO); Las Termas, *Legname 5* (CAS). CORDOBA: Km 969, Dept. Ischilin, *Brizuela 897* (SMU). MENDOZA: Rancho de Tofora, 500 m, *Ruíz Leal 9021* (ARIZ).

This species also has been reported from the Argentinean states of La Rioja and Entre Rios (Descole, *et al.*, 1939) and *San Luis* (Ruíz Leal, 1947).

TAXONOMY. Svenson (1946b) considered *Kallstroemia tucumanensis* to be conspecific with *K. adscendens*, but the two are distinct. The latter is endemic to the Galápagos Islands, Ecuador.

RELATIONSHIPS. *Kallstroemia tucumanensis* is most closely related to the more northerly *K. pubescens*. The latter differs from *K. tucumanensis* in having mostly three pairs of leaflets, flowers 9–15 mm in diameter, obovate petals 6–11 mm long and 5–8 mm wide that are usually white, anthers and pollen only occasionally yellow, a pyramidal ovary, a densely appressed short-pilose fruit with a beak 5–8 mm long, and an obscurely ten-lobed stigma.

5. **Kallstroemia hirsutissima** Vail in Small, Fl. SE. U. S. 670. 1903

TYPE: New Mexico, Dona Ana Co.: plains S White Sands. elev. 4200 ft. 28 August 1897, *E. O. Wooton 564* (NY, holotype; MO, NY, US, isotypes).

Annual; *stems* prostrate, 1.5–7 dm long, copiously sericeous and hirsute with white or gray apically-directed trichomes, forming a dense carpet-like mat; *stipules* 3–6 mm long, ca. 1 mm wide; *leaves* obovate, 1–4 cm long, 2–4 cm wide, copiously and conspicuously pubescent; *leaflets* 3–4 pairs, broadly elliptical to oblong-ovate or broadly ovate, densely hirsute and conspicuously ciliate, veins and margins sericeous, 12–19 mm long, 5-11 mm wide, terminal pair largest; *peduncles* shorter than subtending leaves, thickened distally, 5–12 mm long, curved or straight in fruit; *flowers* pentamerous, less than 1 cm in diameter; *sepals* subulate. 2.5–4 mm long, ca. 1 mm wide, hirsute and sparingly strigose, in flower ca. as long as style, in fruit clasping mature mericarps and ca. 1/2 as long as them, only scarious margins becoming involute, persistent; *petals* yellow, fading white or orange, obovate, 2–4 mm long, ca. 1.5 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid, less than 1 mm in diameter, they and pollen yellow; *ovary* globose, pubescent, ca. 1 mm in diameter; *style* very short, ca. 1/3–1/2 as long as ovary, stout, broadly conical, pubescent; *stigma* more or less clavate, appearing almost sessile on ovary, 10-ridged, papillose; *fruit* broadly ovoid, 4–5 mm high, 6–8 mm wide, strigillose; *beak* 1–4 mm long, shorter than fruit body, hirsute with short white trichomes to stigma base, conical above, base broadly conical; *mericarps* 4 mm high, ca. 1 mm wide, abaxially prominently tubercled, sides pitted, adaxial edge angled. *Fig. 5a, 5b. Map 7.*

FLOWERING DATES. Following the summer rains from June to October, but mainly from July to September.

DISTRIBUTION AND HABITAT. Chihuahuan Desert and adjacent areas of semiarid grassland from southeastern Arizona to Tamaulipas and southern Texas *(Map 7)*. Found from sea level to about 1700 m, mainly at higher elevations. Sympatric with *Kallstroemia californica, K. grandiflora, K. parviflora,* and *K. perannans,* and slightly overlapping with *K. maxima* and *K. rosei* in Nuevo Leon and Tamaulipas.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia hirsutissima* has

copiously pubescent stems which form a dense carpet-like mat, obovate leaves, three to four pairs of conspicuously ciliate leaflets, yellow flowers less than 1 cm in diameter, hirsute and sparingly strigose sepals which clasp the mature mericarps, only their scarious margins becoming involute, a stout broadly conical very short style that is ⅓–½ as long as the ovary, the more or less clavate ten-ridged stigma appearing almost sessile on the ovary, a broadly ovoid strigillose fruit 4–5 mm high and 6–8 wide, and a conical beak 1–4 mm long, hirsute with a ring of short white trichomes. *K. hirsutissima* is unlikely to be confused with any other species of the genus growing in the same area.

SPECIMENS EXAMINED. UNITED STATES. ARIZONA. Pima Co.: Tucson, *Lemmon,* Oct 1880 (MO). Santa Cruz Co.: near Elgin, *Peebles, Harrison & Kearney 3349* (ARIZ, US). Cochise Co.: Benson, *Harrison 8227* (ARIZ, US); Douglas, *W. W. Jones,* 12 Sept 1948 (RSA); San Bernardino Ranch, *Mearns* 597 (US). NEW MEXICO. Locality unknown: east side Rio Grande, *Wright 912* (BM, GH, US). Chaves Co.: 20 mi. S of Roswell, *Earle & Earle 307* in part (POM). TEXAS. Locality unknown: Pecos Valley, *Havard,* Sept 1881 (F, US); Lander, *Knicker,* 24 June 1916 (GH, TEX); Ft. Stockton to Alpine, *Tharp,* 18 Aug 1935 (GH, MO, UC). Jeff Davis Co.: Ft. Davis, *M. S. Young,* 5 Sept 1918 (TEX). Brewster Co.: Alpine, *Tharp 3512* (TEX, US). Dimmit Co.: without locality, *Tharp,* 24 June 1941 (GH, MO, TEX). Kerr Co.: Kerrville, *Cook 17, 19* (LL). Kinney Co.: creek bottom 6 mi. E of Bracketville, gray-brown calcareous silt, *Shinners 30833* (SMU). Bexar Co.: San Antonio, *Ball 908* (US), *Cook,* 1906 (LL), *Havard 1704* (MO), *Schulz 783* (US). Duval Co.: San Diego, *Croft 198* (NY). Cameron Co.: Brownsville, open grounds and dry fields, clay soil, 10 m, *Runyon 1857* (US); Santa Ana National Wildlife Refuge, gravel pile, *Fleetwood 3839* (TEX).

MEXICO. LOCALITY UNKNOWN: Limpia Valley, *Edwards 78* in part (MICH). CHIHUAHUA: 10 km. E of Barreal, dry sandy hillsides, *Stewart 662* (GH); 25 mi. SE of Camargo, 4500 ft, *Shreve 8874* (ARIZ, GH); between Casas Grandes and Sabinal, 5000–5500 ft, *Nelson 6376* (MICH, NY, US); Chihuahua, *LeSeuer* 253 (GH, SMU); hills and plains near Chihuahua, *Pringle 679* (BM, CAS, F, MICH, NY, PH, RSA, US); 5 mi. E of Ciudad Jiménez, ca. 4500 ft, *S. S. White 2143* (GH, MICH); Cuauhtémoc, *LeSeuer* 253 (F, TEX); broad valley 25 km. NW of Jaco toward Victoria, silty flat, *Stewart 678* (GH); 5.5 mi. S of Ojinaga toward Alamos Chapo, outwash from saline shales, *Johnston 8004* (GH). COAHUILA: arroyo between Grutas Villa Garcias SW of Saltillo, ca. 5500 ft, *Bell & Duke 16578* (MO); NE margin of Laguna de Leche, flooded soil, *Johnston 8595* (GH); Llano de Guaje, margins of playa between Lomas del Aparejo and Tanque La India, *Johnston & Muller 788* (GH); 2 km. E of Tanque La India, flats in bottom of bolson, *Stewart 1166* (GH); 12 mi. N of Monclova toward Piedras Negras, silty mesquite thicket, *Johnston 7190* (GH, US); valley floor E of Puerto del Caballo toward Tanque Jerico, barreal, *Johnston 8335D* (GH); valley between low hills 15 mi. S of Sabinas, *Waterfall 16656* (SMU, UC); dry valley floor 10–15 km. E of San Antonio toward Buenavista, savanetta, *Johnston,* 21 Aug 1941 (GH); 5 mi. NW of Zenzontle toward

San José, sabaneta, *Johnston & Muller 971* (GH). NUEVO LEON: Monterrey, *Edwards s. n.* (NY); near Monterrey, *Edwards 140* in part (MICH); desert 21 mi. W of Monterrey, along arroyo, *Waterfall & Wallis 13182* (SMU); along highway 40 mi. S of Monterrey, *Drushel 9327* (NY). TAMAULIPAS: 0.5 mi. S of Huisachal, *Stanford, Lauber & Taylor 2172* (GH, NY, US); near Victoria, ca. 320 m, *Palmer 218* in part (MO). SAN LUIS POTOSI: Las Palmas, *Rose & Hough 4877* (US).

COMMON NAME. Carpetweed.

RELATIONSHIPS. *Kallstroemia hirsutissima* is most closely related to *K. curta*, a species of Hispaniola and the southern islands of the Netherlands Antilles. The latter differs in having usually three pairs of leaflets, the sepals spreading from the base of the mature fruit, and their margins becoming sharply involute, white to yellow-orange petals, a style about as long as the ovary, and the ovoid fruit 4–5 mm in diameter with the strigose beak 1½–2 mm long.

6. **Kallstroemia curta** Rydb. in Boldingh, Fl. Nederland. West-Ind. Eilanden 230. 1913

TYPE: West Indies, Curaçao: rocky coastal hill, St. Joris Bay, prostrate branches 8 dm long; 20–27 March 1913, *N. L. Britton & J. A. Shafer 3096* (NY, lectotype; F, PH, US, isotypes). This name usually is attributed to "Rydb. in Boldingh. Fl. Dutch West Ind. Islands **2**:45. 1914.", but the above citation is its first valid publication. No specimens were cited in the 1913 publication, but three were listed in 1914. Of these three, *Britton & Shafer 3096* at NY bears the word "Type" in Rydberg's handwriting. Therefore, it is confirmed to be the lectotype.

Kallstroemia incana Rydb. in Britt., Bull. Torr. Bot. Club **51**:3. 1924. TYPE: West Indies, Dominican Republic: Barahona, sea level, flower yellow, July 1910, *Fr. Miguel Fuertes 418* (NY, holotype; GH, IJ, MO, US, isotypes).

Annual; *stems* prostrate, 2–3 dm (rarely to 1 m) long, hirsute and sericeous with white apically-directed trichomes, usually forming a dense carpet-like mat; *stipules* 2–4 mm long, ca. 1 mm wide; *leaves* obovate, 1–4 cm long, 2–3 cm wide, usually appearing grayish because of dense pubescence; *leaflets* 3(–4) pairs, ovate, densely appressed-hirsute, veins and margins sericeous, becoming glabrate, 9–15 mm long, 5–10 mm wide, terminal pair largest; *peduncles* shorter than leaves, 2–3 mm long in flower, in fruit 2–13 mm long and curved or straight; *flowers* pentamerous, less than 1 cm in diameter; *sepals* subulate, 2.5–4 mm long, 1–2 mm wide, hirsute and strigose, longer than style in flower, shorter than beak and spreading from base of mature fruit, margins becoming sharply involute, persistent; *petals* white to yellow-orange, elliptical to obovate, 3–4 mm long, marcescent; *stamens* as long as style; *anthers* globose, much less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, ca. 1 mm in diameter, pubescent; *style* ca. as long as ovary, stout, conical, strigose; *stigma* clavate, 10-ridged, less than 1 mm long, papillose; *fruit* ovoid, 4–5 mm in diameter, strigillose; *beak* 1.5–2 mm long, stout, conical above, base widely conical, strigose; *mericarps*

3 mm high, ca. 1 mm wide, abaxially tubercled, sides pitted, adaxial edge angled. *Fig. 6a, 6b. Map 8.*

FLOWERING DATES. Known to flower in March in Curaçao and in July in Cuba, but flowering from January through October in Hispaniola. As in the other Caribbean species, seed germination, plant growth, and flowering probably take place at any time of the year following sufficient rainfall and appropriate temperatures.

DISTRIBUTION AND HABITAT. Disturbed areas from sea level to 1300 m, mainly at lower elevations. Apparently native to Hispaniola and introduced into Cuba and the Netherlands Antilles *(Map 8)*. Sympatric with *Kallstroemia maxima* in Hispaniola and Cuba, and with *K. pubescens* in the Netherlands Antilles.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia curta* may be recognized by its stems forming a dense carpet-like mat, which appears grayish because of the dense pubescence, obovate leaves, usually three pairs of densely pubescent leaflets, white to yellow-orange flowers less than 1 cm in diameter, hirsute and strigose sepals which spread from the base of the mature fruit and have sharply involute margins, clavate ten-ridged stigma, and ovoid strigillose fruit with a conical beak 1½–2 mm long. This species is apt to be confused with *Kallstroemia pubescens* in the southernmost part of its range. The latter may be distinguished by its more upright open habit, peduncles 1–3½ cm long in fruit, usually white flowers 9–15 mm in diameter, hispidulous sepals, pyramidal ovary, capitate obscurely ten-lobed stigma, and densely appressed short-pilose fruit with a beak 5–8 mm long.

SPECIMENS EXAMINED. CUBA. ORIENTE: Estación Naval de Caimanera, *Bro. Hioram 3958* (US).

HAITI. NORD-OUEST: near Bassin Bleu, road to Port de Paix, roadbed, *Leonard & Leonard 14729* (US); near Le Mole St. Nicolas, Mole gorge, rock crevices, *Leonard & Leonard 13322* (US); Presquîle du Nord-Ouest, *Ekman H4038* (US). ARTIBONITE: Cap St. Marc, railroad track near lighthouse, *Ekman H6652* (A); road SE of Gros Morne, ca. 235 m, *Leonard 9972* (GH, NY, UC, US); near Ennery, Puilboreare road, *Leonard 8813* (GH, NY, UC); Hinche, Savane-Papaye, 225 m, *Ekman H6011* (IJ, US). OUEST: Port-au-Prince, Plaine de Léogane, *Buch 1173* (IJ).

DOMINICAN REPUBLIC. SANTIAGO: Hato del Yaque, fields, *Ekman H15981* (US); Valverde, *Uniola* savannah, ca. 100 m, *Ekman H13107* (US). AZUA: San Juan, fields, *Ekman H13395* (A, US). BARAHONA: Rincon, 25 m, *Fr. Fuertes 1352* (NY, US); near Rincon, 1300 m, *Fr. Fuertes 1353* (GH); La Salina, decomposed salt rock, *Howard & Howard 8410* (GH, NY, US).

CURAÇAO. Without locality, *Read s.n.* (PH).

Boldingh (1914) reports *Kallstroemia curta* from the island of Aruba, and Arnoldo (1964) records it from this island and also from Bonaire, but the only specimens I have seen from the southern Caribbean are those from Curaçao cited above.

COMMON NAMES. No common names have been recorded for this species in Cuba or Hispaniola. However, in Aruba, Bonaire, and Curaçao it is known by the same names as is *Kallstroemia pubescens:* Angglo Boobo or Anglo Bobo.

TAXONOMY. In publishing *Kallstroemia incana,* Rydberg indicated its affinities with *K. curta,* but stated that it differed in being "more canescent, more branched, with shorter internodes and smaller leaves, and the beak different, not at all swollen." Except for the beak, these differences all are of vegetative characters that prove to be very plastic in all species of the genus where environmental conditions vary. Upon examination of the specimens cited above, all differences given by Rydberg and others, both of a vegetative and floral nature, overlap between the populations in Hispaniola and Cuba and those from Curaçao. The more northerly collections tend to be more pubescent than those from Curaçao, but this single difference hardly makes them worthy of taxonomic recognition, even at the subspecific level.

RELATIONSHIPS. *Kallstroemia curta* is most closely related to *K. hirsutissima,* a species of northern Mexico and the southwestern United States. *Kallstroemia hirsutissima* differs in having three to four pairs of leaflets, hirsute and sparingly strigose sepals which clasp the mature mericarps, with only their scarious margins becoming involute, yellow petals, a very short stout broadly conical style that is ⅓–½ as long as the ovary, the stigma appearing to be almost sessile on the ovary, and a broadly ovoid strigillose fruit that is 4–5 mm high and 6–8 wide, with a 1–4 mm long beak which is hirsute with a ring of short white trichomes.

7. **Kallstroemia adscendens** (Anderss.) Robins., Proc. Amer. Acad. 38:156. 1902

Tribulus adscendens Anderss., Svensk. Vet-akad. Handl. **1853**:245. 1854. TYPE: Ecuador, Galápagos Islands: "Hab. locis graminosis, siccis regionis inferioris insularum Chatham et Charles (Ipse)," *N. J. Andersson s. n.* (holotype presumably at S, not seen; GH, isotype).

Tribulus maximus var. *adscendens* (Anderss.) Anderss., *op. cit.* **1857**:107. 1861. I follow Rose (1892) and Robinson (1902) in assuming that Andersson intended to make this combination, although his citation might lead one to the conclusion that he considered *T. adscendens* to be a synonym of *T.*

maximus. This is a valid assumption, as Andersson later (1861b) referred to this taxon as "*T. maximus* var. A.", A. indicating "of Andersson."

Annual; *stems* prostrate to decumbent, to several dm long, sericeous and hirsute with apically-directed white trichomes; *stipules* 3–4 mm long, ca. 1 mm wide; *leaves* elliptical, to ca. 2 cm long and 1 cm wide; *leaflets* 2–3 pairs, oblong to subfalcate, appressed-hirsute, veins and margins sericeous, to almost glabrate, 9–18 mm long, 3.5–7 mm wide, penultimate pair largest; *peduncles* in fruit longer than subtending leaves and sharply bent at base and straight above, slightly thickened distally, 5–21 mm long; *flowers* pentamerous, less than 1 cm in diameter; *sepals* subulate, 3–3.5 mm long, ca. 1 mm wide, little shorter than petals, hirsute and strigose, longer than style in flower but not extending beyond tops of mature maricarps in fruit, spreading from base of mature fruit and margins becoming sharply involute, persistent; *petals* yellow, obovate, ca. 4 mm long, 2–3 mm wide, marcescent; *stamens* as long as style; *anthers* globose, much less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, ca. 1.5 mm in diameter, strigose; *style* ca. 1 mm long, stout, conical, strigose; *stigma* clavate, 10-ridged, less than 1 mm long, papillose; *fruit* ovoid, 3–4 mm in diameter, strigose; *beak* ca. 2 mm long, ca. 1/2 as long as fruit body, conical, strigose; *mericarps* ca. 3 mm high and 1 mm wide, abaxially cross-ridged and tubercled, sides pitted, adaxial edge angled. *Fig. 7a, 7b. Map* 9.

FLOWERING DATES. Known to flower from April through June, during the last half of the rainy season.

DISTRIBUTION AND HABITAT. Endemic to the Galápagos Islands, Ecuador *(Map 9)*. Found on the beaches and lower slopes of the arid coastal zone of the islands.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia adscendens* may be recognized by its elliptical leaves, two to three pairs of leaflets, fruiting peduncles longer than the subtending leaves, yellow flowers less than 1 cm in diameter, hirsute and strigose sepals spreading from the base of the mature fruit, with the margins becoming sharply involute, and tubercled strigose fruit with the beak about ½ as long as the fruit body.

SPECIMENS EXAMINED. LOCALITY UNKNOWN. *Andersson s. n.* (NY), 1852 (MO).

BARRINGTON ISLAND. Bahía de Barrington, NE part of island, in stony ground, ca. 325 ft, *Snow 113* (DS). Along intermittent water course 1/4 mi inland to SW from NE corner of island, *Wiggins & Porter 587* (CAS).

CHAMPION ISLAND. Without locality, *Wiggins & Porter 513* (CAS).

CHARLES ISLAND. Post Office Bay, beach and environs at E end, *Wiggins & Porter 558* (CAS).

CHATHAM ISLAND. Punta Pitt, *Snow 244* (DS). Along road from Wreck Bay to El Progreso, *Wiggins & Porter 368* (CAS).

DUNCAN ISLAND. Without locality, Agassiz, 2 Apr 1891 (GH, US). Lower slopes, middle eastern part of island, *Howell 9819* (CAS, GH).

GARDNER ISLAND. Without locality, *Snodgrass & Heller 615* (DS. GH). Common over much of island, *Wiggins & Porter 473* (CAS).

HOOD ISLAND. Without locality, *Snodgrass & Heller 756* (GH). On beach, Gardner Bay, *Howell 8653* (CAS). Along S side of Punta Suárez. *Wiggins & Porter 489* (CAS). W end inland from Punta Suárez. *Wiggins & Porter 457* (CAS).

VARIATION. Although Andersson described *Kallstroemia adscendens* as having a five-carpellate fruit with two single-seeded locules per carpel, examination of available material shows this species to be a typical *Kallstroemia* with ten one-seeded mericarps.

RELATIONSHIPS. Robinson (1902) was the first to suggest the close relationship of *Kallstroemia adscendens* and the North American *K. californica* (as *K. brachystylis*). The latter may be distinguished from *K. adscendens* by its hirsute and strigose stems, three to seven pairs of leaflets, fruiting peduncles shorter than the subtending leaves, usually deciduous sepals, strigillose fruit with prominent tubercles that may reach 1½ mm in length, and cylindrical beak that is little shorter than the fruit.

8. **Kallstroemia californica** (S. Wats.) Vail, Bull. Torr. Bot. Club **22**:230. 1895

Tribulus californicus S. Wats., Proc. Amer. Acad. **11**:125. 1876. TYPE: Mexico, Baja California: eastern side of the peninsula, 1870, *Palmer s. n.* (GH, holotype). As indicated elsewhere (Porter, 1963), the type probably was collected in January or February, 1870, in southern Baja California.

Kallstroemia brachystylis Vail, Bull. Torr. Bot. Club **24**:206. 1897. TYPE: New Mexico, Dona Ana Co.: mesa near Las Cruces, alt. 3900, 12 August 1895, *E. O. Wooton s. n.* (NY, holotype; GH, isotype).

Tribulus brachystylis (Vail) Robins. in Gray, Syn. Fl. N. Amer. **1**:354. 1897.

Kallstroemia californica var. *brachystylis* (Vail) Kearn. & Peeb., Jour. Wash. Acad. Sci. **29**:485. 1939.

Annual; *stems* prostrate to decumbent, 1–6.5 dm long, hirsute and strigose with apically-directed white trichomes, becoming glabrate; *stipules* 1.5–5 mm long, ca. 1 mm wide; *leaves* elliptical to occasionally obovate, 1.5–6 cm long, 1–3 cm wide; *leaflets* 3–6(–7) pairs, elliptical to oval, appressed-hirsute, veins and margins sericeous, becoming glabrate, 4–17 mm long, 1.5–9 mm wide, middle pairs largest; *peduncles* shorter than subtending leaves, thickened distally, to 15 mm long in flower, in fruit 8–33 mm long and bent sharply at base and straight above; *flowers* pentamerous, to 1 cm in diameter; *sepals* lanceolate, 2–4 mm long, 1–1.5 mm wide, strigose or hirsutulous and strigillose, margins become involute, usually deciduous, if persistent spreading from base of mature fruit and not reaching tops of mature mericarps; *petals* yellow, drying white or orange, obovate, 4–6 mm long, 2.5–3 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid.

less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, ca. 1 mm in diameter, pubescent; *style* shorter than ovary, stout, conical, strigillose; *stigma* clavate, 10–ridged, less than 1 mm long, papillose; *fruit* ovoid, 3–5 mm wide including tubercles, to 4 mm high, strigillose; *beak* 2–4 mm long, shorter than fruit body, cylindrical, base conical, glabrous or base sparingly strigillose; *mericarps* ca. 3 mm high and 1 mm wide, abaxially with 4–5 blunt oblong tubercles that may reach 1.5 mm long, tubercles becoming more prominent as fruits mature, sides pitted or smooth, adaxial edge angled. *Fig. 8a, 8b. Map 10.*

FLOWERING DATES. Following summer rains (mainly July through October) through most of the range, but occasionally beginning in March in Texas, and August through March (following both fall and winter rains) in Baja California.

DISTRIBUTION AND HABITAT. Flat sandy and disturbed areas of the Sonoran Desert across the northern Chihuahuan Desert to the semiarid grasslands of Tamaulipas and southern Texas; also along the west coast of Mexico to southern Sinaloa and the Tres Marias Islands, and extending into northern Arizona and southern Baja California *(Map 10)*. Found from sea level to about 1600 m, mainly at lower elevations. Sympatric with *Kallstroemia grandiflora, K. hirsutissima, K. parviflora, K. peninsularis,* and *K. perennans,* and slightly overlapping in the southwest with *K. maxima* and *K. pubescens* and in the southeast with *K. maxima* and *K. rosei.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia californica* is easily recognized by the combination of its hirsute and strigose stems, usually elliptical leaves, three to seven pairs of leaflets, fruiting peduncles shorter than the subtending leaves, yellow flowers less than one centimeter in diameter, usually deciduous sepals, strigillose fruit with prominent tubercles that may reach 1½ mm in length, and a cylindrical beak that is little shorter than the fruit body. Although there may be some overlap in these characteristics with other species in the same geographical area, in combination they readily distinguish *Kallstroemia californica* from its congeners.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. CALIFORNIA. San Bernardino Co.: Conrise Valley, sands, *Jaeger,* 15 Sept 1925 (POM); 8 mi W of Ludlow, *Ferris 1326* (DS). Riverside Co.: hay fields, *M. E. Jones 24963* (CAS, GH, MO, NY, POM, UC); Palm Springs, *M. E. Jones,* 7 Sept 1925 (DS). San Diego Co.: SW part of Colorado Desert, *Orcutt,* 8 Oct 1890 (US). Imperial Co.: Heber, *Abrams 4002* (DS, F, GH, MO, NY, POM); sand dunes N of Picture Rocks, *Reed 6697* (POM). ARIZONA. Mohave Co.: Ash Creek, near Sandy River, *Braem 563* (DS).

Coconino Co.: Havasupai Canyon, fields and waste places, *Clover 7065* (ARIZ, MICH), *7138* (MICH); W bank of Colorado River 1.5 mi below Lee's Ferry, 3800 ft, *Cutler 3149* (DS, GH, MO, NY). Yavapai Co.: Verde, *W. W. Jones*, 23 July 1920 (UC, US). Gila Co.: San Carlos, *Hoyt*, Aug 1892 (NY). Yuma Co.: near Mohawk, *Peebles, Harrison & Kearney 4924* (ARIZ, US); Yuma, mesas and depressions, *Thornber*, 24 Sept 1912 (ARIZ, UC). Maricopa Co.: Litchfield, *Peebles, Harrison & Kearney 4525* (ARIZ). Pinal Co.: near Phoenix, roadsides, *Kearney 123* (US); Sacaton, *Peebles 10597* (ARIZ, POM, US). Pima Co.: 4 mi W of Mission San Xavier, near shallow arroyo, *Wiggins & Rollins 57* (ARIZ, DS, GH, MICH, MO, NY, US); Tucson, 2400 ft, *Thornber 234* (ARIZ, DS, MO, NY, POM, UC). Graham Co.: Clifton, *Davidson 17* (DS). Santa Cruz Co.: hills near Nogales, *Peebles, Harrison & Kearney 5568* (ARIZ, US). Cochise Co.: Dos Cabezas, *Orcutt 2229* (MO); San Simon, *Thornber 5682* (ARIZ). NEW MEXICO. Grant Co.: Red Rock, *Goldman 1539* (US). Luna Co.: Nutt, 1420 m, *Eggleston 16262A* (US). Dona Ana Co.: Mesilla Valley, ca. 3850 ft, *Wooton & Standley 3189* (ARIZ, DS, F), *27249* (WIS); Organ Mts., *Wooton 422* (DS, MO, NY, POM, UC, US). Eddy Co.: sandhills near Loving, *Standley 40357* (US). TEXAS. El Paso Co.: desert near El Paso, *Knobloch 199* (MSC). Hudspeth Co.: between Nulo and Harris Siding, *Ferris & Duncan 2449* in part (MO). Presidio Co.: Presidio, *Trelease 311* (MO). Brewster Co.: near San Vicente, muddy bank of Rio Grande, *Young*, 26 Aug 1915 (TEX). Kerr Co.: Kerrville, *Cook 20* (LL), *20A* (LL, NY). Kinney Co.: 17 mi E of Del Rio, *Shreve 8387* (ARIZ). Bexar Co.: San Antonio, *Berlandier 2541* in part (WIS). Lavaca Co.: Hallettsville, *Fisher 109* (US). Atascosa Co.: 13.6 mi S of Jordanton, silty clay roadside, *Shinners 16953* (SMU). La Salle Co.: US Highway 81, 13 mi N of Encinal, orange-brown sand, *Solis 56* (SMU). Live Oak Co.: George West, sandy loam, *Schiller 950* (US). San Patricio Co.: 7.5 mi S of Taft, sandy loam, *F. B. Jones 491* (SMU). Aransas Co.: Aransas Refuge, *Blakey 43* (GH). Webb Co.: Laredo, *Palmer 131* in part (F, MICH, NY). Duval Co.: Colmena Creek, saline soil, *Correll & Johnston 19737* (LL). Kleberg Co.: Kingsville, dry neglected soil in disturbed areas, *Bogush 11845* (ARIZ, US). Zapata Co.: San Ygnacio, *Tharp 3517* (TEX, US). Jim Hogg Co.: State Highway 359, 5 mi W of Hebronville, loose pale orange sand, *Ramirez, Alva & McCart 8717* (SMU, TEX). Starr Co.: US Highway 83 below Falcon Dam, fine sandy silt, *Garza Gongora, de Anda & McCart 8465* (LL, SMU, TEX). Hidalgo Co.: Rio Grande Valley, *Walker 67* (GH, LL, TEX, UC). Willacy Co.: Sauz Ranch, sandy loam, *Johnston & Davis*, 23 Nov 1953 (TEX). Cameron Co.: Brownsville, open ground, *Runyon 2021* (F), *5804* (LL); Rio Hondo, *Chandler 7067* (GH, MO, NY, UC, US).

MEXICO. BAJA CALIFORNIA NORTE: 15 mi N of Bahía de San Luis Gonzaga, granitic sand, *Wiggins 16037* (DS, MICH, TEX); open sandy area near S end of Laguna Chapala, ca. 2200 ft, *Thomas 8201* (CAS, DS). BAJA CALIFORNIA SUR: ca. 6 mi N of Cuarenta, sandy coastal plain, *Thomas 8362* (ARIZ, CAS, DS, GH, UC, US); 8.5 mi N of La Paz toward Bahía Pichilingue, rocky red volcanic soil at roadside, *Porter 384* (ARIZ, CAS, DS, MEXU, UC); San José del Cabo, *Brandegee*, Sept 1891 (DS, GH, NY, US). SONORA: Agiabampo, *Palmer 786* (GH, MICH, NY, US); Guaymas, waste places, *Palmer 107* (BM, GH, MICH, NY, US); 27 mi W of Hermasillo toward Bahía Kino, *Wiggins & Rollins 130* (ARIZ, DS, GH, MICH, MO, NY, UC, US). CHIHUAHUA: Colonia Juarez, *M. E. Jones*, 11 Sept 1903 (POM); Ramos, open grassland, 4800 ft, *Leopold 257* (UC). COAHUILA: Monclova, *Palmer 131A* (US); Sabinas, *Kenoyer 32* (F).

TAMAULIPAS: Papalote de Mirandena, prairie on sandy loam shallowly overlying caliche, *Crutchfield & Johnston* 5552 (MEXU, MICH, TEX); near Victoria, ca. 320 m, *Palmer 218* in part (F, GH, NY, UC, US). SINALOA: rocky areas 12–15 km SE of Mazatlán, wet soil along road, 25 m, *Worth & Morrison 8812* (GH, MO, UC, US); Porvenir and Norote, 10 m, *Gonzalez Ortega* 5889 (DS, GH, PH, US). DURANGO: ca. 3 mi W of Durango, *Hevly, Martin & Arms,* 1 Aug 1960 (ARIZ). NAYARIT: Isla María Madre, edge of beach near penal colony, *Ferris* 5624 (DS, US). SAN LUIS POTOSI: locality unknown, *Schaffner,* 1876 (NY).

COMMON NAME. Golondrina (Nayarit, Sinaloa, and Sonora, Mexico).

TAXONOMY. The name *Kallstroemia brachystylis* has been applied to those specimens with fewer leaflets and less pronounced tubercles on the fruits than is usual for this species. However, Kearney and Peebles treating *K. brachystylis* as a variety of *K. californica,* pointed out that there was much intergradation in these characters. An examination of a number of collections made throughout the range of *K. californica* shows that variation in these characters is continuous, and there is no real justification for the recognition of two taxa.

In the past, confusion has led to the recognition of two taxa. This confusion arose largely from the determination of a number of collections (usually immature or depauperate specimens) of *Kallstroemia parviflora* as *K. brachystylis.* Such determinations include at least two specimens (at NY and US) with the same locality and date as the type specimen of *K. brachystylis.*

VARIATION. As indicated above, there may be considerable variation in leaflet number (three to seven pairs) and fruit tubercles (blunt, oblong, and 1½ mm long to less prominent), but this variation is of a continuous nature. Another character which occasionally shows marked variation is leaf shape. Although the overwhelming number of specimens have elliptical leaves, with the middle leaflets largest, some individuals have obovate leaves, with the terminal leaflets largest, and still others may have leaves of both shapes.

Watson (1876); Brewer *et al.* (1876); and Gray (1887) have stated that *Kallstroemia californica* has five two-loculed and two-seeded carpels and a deeply five-lobed fruit. These statements undoubtedly are due to the only fruit on the holotype specimen (at least the only one now present) having the alternate carpels abortive and superficially appearing five-lobed. Close inspection shows it to be ten-lobed, typical for the genus. All the mature

mericarps of this species examined proved to be one-seeded, also typical for the genus.

RELATIONSHIPS. *Kallstroemia californica* appears to be closely related to *K. adscendens* from the Galápagos Islands, Ecuador, and perhaps to *K. standleyi* from Oaxaca, Mexico. *Kallstroemia adscendens* differs in having hirsute and sericeous stems, two to three pairs of leaflets, fruiting peduncles longer than the subtending leaves, persistent sepals, a strigose fruit with much less prominent tubercles, and a conical beak about ½ as long as the fruit body. *Kallstroemia standleyi* may be distinguished by its densely sericeous and sparingly hirsute stems, fruiting peduncles longer than the subtending leaves, persistent sepals, yellow-orange petals 10–12 mm long, linear-oblong anthers, style longer than the ovary, oblong stigma, and broadly ovoid strigose fruit 5–6 mm high and 7–10 wide, including the elongate blunt or slightly fungoid tubercles, which may be to 2 mm long.

9. **Kallstroemia standleyi** D. M. Porter, *sp. nov.*

TYPE: Mexico, Oaxaca: sand dunes along beach, 0.5 mi E of Salina Cruz, petals yellow-orange, 10–12 mm long; 16 July 1946, *Thomas Morley 681* (GH, holotype; F, MO, UC, US, isotypes). This species is named in honor of Paul Carpenter Standley (1884-1963), prolific writer on the flora of the Americas and student of the *Zygophyllaceae.*

Annua; caules prostrati, 1.5–2 dm longi, dense sericei, sparse hirsuti, trichomata alba, antrorsa; stipulae 3–4 mm longae, 1–1.5 mm latae; folia elliptica, 2–3 cm longa, 1–1.5 cm lata; foliolorum pares 4–6, elliptica vel anguste ovata, sericea, 8–11 mm longa, 3–4.5 mm lata, pares in medio laminae maxima; pedunculi quam folia subtendentia longiores, ad apicem incrassati, ad anthesin 2.5–3 cm longi, in fructu 2.5–3 cm longi et curvati; sepala anguste ovata, 5–8 mm longa, 2–3 mm lata, in fructu quam mericarpia longiora, quam rostrum breviora, in fructu e basi patentia, margines deinde involuti, persistentia; petala luteo-aurantiaca, 10–12 mm longa, late obovata; stamina et stylus aequilongus; antherae lineari-oblongae, 4 mm longae, antherae et pollen luteum; ovarium ovoideum, 1.5–2.5 mm in diametro, pubescens; stylus 3–3.5 mm longus, cylindricus, ad basin strigosus; stigma oblongum, 1 mm longum, 10-porcatum, papillosum; fructus late ovoideus, 5–6 mm altus, 7–10 mm latus (tuberculis inclusis), strigosus; rostrum 4–5 mm longum, quam fructificatio 1/2 brevius, cylindricum, ad basin conicum strigosumque; mericarpia 5 mm alta, ca. 1 mm lata, abaxialiter pluritubercu-lata, tubercula ad 2 mm longa, obtusa ad fungoidea, elongata, in maturitate prominentiora, latera foveolata, adaxialiter recta.

Annual; *stems* prostrate, 1.5–2 dm long, densely sericeous and sparingly hirsute with white apically-directed trichomes; *stipules* 3–4 mm long, 1–1.5 mm wide; *leaves* elliptical, 2–3 cm long, 1–1.5 cm wide; *leaflets* 4–6 pairs, elliptical to narrowly ovate, sericeous, 8–11 mm long, 3–4.5 mm wide, middle pairs largest; *peduncles* longer than subtending leaves, thickened distally, 2–2.5 cm long in flower, 2.5–3 cm long and curved in fruit; *sepals* narrowly

ovate, 5–8 mm long, 2–3 mm wide, sericeous, spreading from base of mature fruit and longer than mericarps but shorter than beak, margins becoming involute, persistent; *petals* yellow-orange, 10–12 mm long, broadly obovate; *stamens* as long as style; *anthers* linear-oblong, 4 mm long, they and pollen yellow; *ovary* ovoid, 1.5–2.5 mm in diameter, pubescent; *style* 3–3.5 mm long, cylindrical, base strigose; *stigma* oblong, 1 mm long, 10-ridged, papillose; *fruit* broadly ovoid, 5–6 mm high, 7–10 mm wide including tubercles, strigillose; *beak* 4–5 mm long, ca. 1/2 to as long as fruit body, cylindrical, base conical and strigose; *mericarps* 5 mm high, ca. 1 mm wide, abaxially with several elongate blunt to slightly fungoid tubercles to 2 mm long, becoming more pronounced as fruit matures, sides pitted, adaxial edge straight. *Fig. 9a, 9b. Map 11.*

FLOWERING DATES. Known to flower in July.

DISTRIBUTION AND HABITAT. Known only from the type locality *(Map 11)*. Both *Kallstroemia maxima* and *K. pubescens* are known from the same general area.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia standleyi* may be distinguished by its elliptical leaves, four to six pairs of leaflets, fruiting peduncles longer than the subtending leaves, sericeous sepals which spread from the base of the mature fruit, their margins becoming involute, yellow-orange petals 10–12 mm long, linear-oblong anthers 4 mm long, cylindrical style longer than the ovary, oblong ten-ridged stigma, broadly ovoid strigose fruit 5–6 mm high and 7–10 wide, including the prominent elongate blunt to slightly fungoid tubercles, which may become 2 mm long, and beak ½ to as long as the fruit body.

RELATIONSHIPS. *Kallstroemia standleyi* appears to be most closely related to the more northerly *K. californica*. The latter differs in having hirsute and strigose stems, fruiting peduncles shorter than the subtending leaves, yellow flowers to 1 cm in diameter, usually deciduous sepals, conical style shorter than the ovary, ovoid strigillose fruit up to 4 mm high and 3–5 wide, including the prominent elongate blunt tubercles, which become 1½ mm long, and the beak shorter than the fruit body.

10. **Kallstroemia boliviana** Standl., Field. Mus. Nat. Hist. Publ. Bot. 11:161. 1936

TYPE: Bolivia, Cochabamba: Cerro San Pedro, Cochabamba, elev. 2600 m, 25 December 1928, *José Steinbach 8784* (F, holotype; BM, GH, MO, NY, US, isotypes).

Tribulus maximus var. *roseus* O. Ktze., Rev. Gen. Pl. 3(2):30. 1898. TYPE: Bolivia, Cochabamba: Parotani, elev. 2400 m, 20 March 1892, *Otto Kuntze s. n.* (NY, holotype; NY, isotype).

Perennial; *stems* prostrate to decumbent, to 5–8 dm long and several dm

high, hirsute and sericeous with white apically-directed trichomes; *stipules* 3–6 mm long, 2–3 mm wide; *leaves* obovate, 2.5–3 cm long, to ca. 2 cm wide; *leaflets* 2–3(–4) pairs, broadly ovate, sericeous, 12–23 mm long, 7–14 mm wide, terminal pair largest; *peduncles* longer than subtending leaves, thickened distally, 7–35 mm long in flower, 8–41 mm long and curved in fruit; *flowers* pentamerous, 2–3 cm in diameter; *sepals* ovate, 6–9 mm long, ca. 2 mm wide, ca. 1/2 as long as petals, hirsute and strigose, longer than style in flower, in fruit clasping and almost entirely covering mature mericarps but shorter than beak, scarious margins may or may not become involute, persistent; *petals* yellow to orange, base darker, fading orange, obovate, 12–19 mm long, 8–18 mm wide, marcescent; *stamens* as long as style; *anthers* globose, ca. 1 mm in diameter, they and pollen red; *ovary* conical, 3–4 mm high, strigose; *style* ca. as long as ovary, narrowly conical, strigose; *stigma* oblong, 10-ridged, 1–2 mm long, papillose; *fruit* ovoid, 5–6 mm in diameter, strigose; *beak* 5–7 mm long, cylindrical, base conical, strigose to stigma base; *mericarps* 4–5 mm high, ca. 1 mm wide, abaxially rugose and margins flattened, sides pitted, adaxial edge angled. *Fig. 10a, 10b. Map 12.*

FLOWERING DATES. October through April, following summer rains.

DISTRIBUTION AND HABITAT. Disturbed areas in the semiarid valleys on the eastern face of the Cordillera Oriental of Bolivia, and known from a single similar locality in Peru *(Map 12)*. Occurring from about 1100 to 2800 m.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia boliviana* may be distinguished by the combination of its perennial habit, obovate leaves, usually two or three pairs of sericeous leaflets, yellow to orange flowers (bases darker) 2–3 cm in diameter, hirsute and strigose sepals that clasp and almost entirely cover the mature mericarps, the scarious margins may or may not become involute, red anthers and pollen, conical ovary, oblong ten-ridged stigma, strigose fruit, with the beak longer than the fruit body, and the mericarps abaxially rugose with flattened margins.

SPECIMENS EXAMINED. PERU. HUANCAVALICA: Río Mantaro Valley, NE of Pampas, 1300–1400 m, *Weberbauer 6516* (US).

BOLIVIA. WITHOUT LOCALITY: *Mandon s. n.* (F). LA PAZ: Cotaña am Illimani, 2500 m, *Buchtein 97* (GH), 2400 m, *671* (BM, F, MO, NY), *3198* (GH, NY, US); San Pedro, near Sorata, 2600–2700 m, *Mandon 857* (GH), *899* (BM, NY). COCHABAMBA: Cerro San Pedro, near Cochabamba, sandy place, 2550 m, *Cárdenas 2260* (GH), hard-packed soils, 2600 m, *Cutler & Cárdenas 10014* (GH); near Cochabamba, *Bang 927* (BM, F, GH, MICH, MO, NY, PH, US); ca. 3 km E of Cochabamba, hillside, 2800 m, *Eyerdam 24902* (GH, UC); ca. 5 km SE of Cochabamba, dried mudflat, 2800 m, *Eyerdam 24901* (F); Coronilla, near cemetery S of Cochabamba, waste soil, 2566 m, *Cutler 7460* (US); Mizque, 2040 m, *Cárdenas 3860* (GH); Panduro, sandy slopes near Río Caine, 1800 m, *Cárdenas 2426* (US); Quioma silver mines, dry red clay soil, slopes, *Eyerdam 25343* (F, UC);

beyond Rosario, dry bank, 8400 ft, *Brooke* 5228 (F, NY); Samaipata, sandy soil, 1120 m, *Cárdenas 3130* (US); Tako Tako, farm near Mizque, edge of cultivated land, 2035 m, *Brooke* 5889 (F, NY); Las Yungas, 6000 ft, *Rusby* 739 (MICH, NY). SANTA CRUZ: Puente Pilato (Morochata), sandy soil, 2600 m, *Cárdenas 4446* (US). TARIJA: Padcaya, 2100 m, *Fiebrig 2511* (GH); outskirts of Tarija, semiarid plain, 1900 m, *West 8290* (GH, MO, UC, US); near Tarija, waste ground, 6600 ft, *Balls B6089* (F, UC, US).

The Peruvian collection, *Weberbauer 6516*, has the same collector's number as specimens of *Kallstroemia parviflora* at F and GH. However, the latter collection was made "below Pampas," while that of *K. boliviana* was made "northeast of Pampas."

RELATIONSHIPS. *Kallstroemia boliviana* is most closely related to the more southerly *K. tribuloides* and perhaps to the more northerly *K. pennellii*. *Kallstroemia tribuloides* differs in its annual habit, sericeous stems, elliptical leaves, three to six pairs of leaflets, occasionally hexamerous orange flowers 1½–2½ mm in diameter, broadly ovate sepals, with the margins not becoming involute, linear-oblong anthers, and glabrous fruits. *Kallstroemia pennellii* has an annual habit, strigose stems, elliptical leaves, three to four pairs of leaflets, fruiting peduncles about 8 cm long, sericeous sepals 15 mm long, with the margins not becoming involute, and longer than the beak in fruit, yellow petals 3 cm long, the fruit strigillose, with a glabrous beak, and the mericarps abaxially cross-ridged and slightly keeled.

11. **Kallstroemia tribuloides** (Mart.) Steud., Nomencl. Bot. ed. 2. 1:844. 1840

The name "*Kallstroemia tribuloides* (Mart.) Wight & Arn., Prodr. 1:145. 1834." commonly is used for this taxon, but as discussed under *K. maxima* and pointed out by Foster (1958) the combination was never made by Wight and Arnott. Steudal was the first to validly publish the combination, incorrectly attributing it to Wight and Arnott.

Ehrenbergia tribuloides Mart., Nov. Gen. Sp. Brasil. 2:73. 1827. TYPE: Brazil, "Crescit in herbosis sabulosis, ad fluvium S. Francisci, prope Joazeiro et alibi in mediterraneis Provinciae Bahiensis," *K. F. P. von Martius* (holotype presumably at BR or M, not seen). There can be no doubt as to the application of this name, due to von Martius' excellent colored illustration of the holotype (his pl. 163).

Tribulus brasiliensis Spreng., Syst. Veg. ed. 16. 4(2):343. 1827. *nom. superfl.* Based on *Ehrenbergia tribuloides*, cited as a synonym.

Annual; *stems* prostrate to decumbent, to 6 dm long, densely sericeous with apically-directed white trichomes, becoming glabrate; *stipules* 4–8 mm long, 1–2 mm wide; *leaves* elliptical, 3–7 cm long, 2–3 cm wide; *leaflets* 3–6 pairs, oval or oblong, appressed-hirsute and sericeous, becoming glabrate, 10–20 mm long, 3–13 mm wide, middle pairs largest; *peduncles* usually longer than subtending leaves and curved in fruit, becoming thickened distally, 1–3.5 cm long; *flowers* pentamerous, rarely hexamerous, 1.5–2.5 cm

in diameter; *sepals* broadly ovate, 6–7 mm long, 2–4 mm wide, ca. 1/3–1/2 as long as petals, hirsute and strigose, in flower as long or longer than style, in fruit clasping and almost entirely covering mature mericarps but shorter than beak, margins not becoming involute, persistent; *petals* orange, basally sometimes darker, obovate, 7–12 mm long, 5–6 mm wide, marcescent; *stamens* as long as style; *anthers* linear-oblong, rarely linear, 1 mm long, they and pollen orange; *ovary* conical, 2–3 mm high, glabrous; *style* 3 mm long, cylindrical, base conical; *stigma* oblong, 10(–12)-ridged, ca. 1 mm long, papillose; *fruit* ovoid, 5–6 mm in diameter, glabrous; *beak* 3–10 mm long, glabrous, cylindrical, base conical; *mericarps* 4–5 mm high, ca. 1 mm wide, abaxially rugose and margins flattened and slightly keeled, sides pitted, adaxial edge curved. *Fig. 11a, 11b. Map 13.*

FLOWERING DATES. November through May following summer rains.

DISTRIBUTION AND HABITAT. Semiarid northeastern Brazil, southern Bolivia, and northwestern Argentina *(Map 13)*. Apparently native to Argentina and Bolivia and introduced into Brazil. Open sandy places, riverbanks, railroad embankments, and roadsides from 300 to 1800 m. Sympatric over much of its range with *Kallstroemia tucumanensis.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia tribuloides* is easily recognized by its combination of densely sericeous stems, elliptical leaves, three to six pairs of leaflets, rarely hexamerous orange flowers 1½–2½ cm in diameter, broadly ovate hirsute and strigose sepals which clasp and almost entirely cover the mature mericarps, the margins not becoming involute, linear-oblong anthers, conical ovary, oblong ten-ridged stigma, glabrous fruit, with the beak usually longer than the fruit body, and the mericarps abaxially rugose with flattened and slightly keeled margins. *Kallstroemia tribuloides* is commonly found growing with (but is not likely to be confused with) the obovate-leaved, small, yellow-flowered, and strigose-fruited *K. tucumanensis.*

SPECIMENS EXAMINED. BRAZIL. PIAUI: Boa Esperança, *Gardner 2084* (BM, GH, NY). BAHIA: Joazeiro, *Curran 252* (GH, US). ALAGOAS: Ilha São Pedro, Rio do São Francisco, open sandy places, *Gardner 1264* (BM, GH, NY).

BOLIVIA. TARIJA: Villamontes, *Pflanz 2001* (US).

ARGENTINA. SALTA: Burela, *Luna 979* (CAS); Metán, *O'Donell 2488* (A); Pasaje del Río Juramento, *Lorentz & Hieronymus 325* (F); El Quebrachal, *Luna 701* (CAS, DS). TUCUMAN: El Cajón, sandy banks of Río Nio, 700 m, *Venturi 8524* (DS, MO); road S of Jarami, *Lillo 2494* (F, GH); Tapia, *Lillo,* Feb 1903 (GH), 750 m, *Venturi 1031,* railroad embankments, 750 m, *1077* in part (US); roadside near Tapia, 820 m, *Mexia 04344* (GH, MO, UC); Tapia to Cadellal, 500 m, *Schreiter 1028* (DS, F, GH. NY, UC); Tapia to Vipos, 750 m, *O'Donell & Lourteig,* 4 Feb 1939 (DS, F, GH,

NY, UC); Vipos, fields, *Lillo 7896* (F, GH), 786 m, *Schreiter 1910* (F), 24 Jan 1926 in part (DS, F, GH, NY, UC). CATAMARCA: Campo del Pilciao, *Schickendantz 168* in part (UC, US); La Florida to Puerta del Corral Quemado, 1800 m, *Schreiter*, 19 Mar 1934 (F, GH); San Isidro to Río del Valle, *Rojas Paz 32* (GH); Sierra de Belén, 1500 m, *Schreiter*, Mar 1939 (F, GH). SANTIAGO DEL ESTERO: El Charco, hard dry soil, 300 m, *Venturi 10395* (BM, MO, NY). LA RIOJA: Río Hondo at road to Cantadero, *Hunziker 5020* (US).

In addition, collections which have not been seen have been reported from the states of Rio Grande do Norte, Brazil (von Luetzelburg, 1923), and Jujuy (Descole, *et al.*, 1940) and Mendoza (Ruíz Leal, 1947), Argentina.

COMMON NAME. Rosa do Campo (Brazil).

VARIATION. Ruíz Leal (1947) reports that specimens of *Kallstroemia tribuloides* from Mendoza, Argentina, had flowers half the size (ca. 1 cm in diameter) and were more reduced in height than those from farther north. These differences probably were due to environmental factors. The collections which he cited have not been seen.

RELATIONSHIPS. *Kallstroemia tribuloides* is most closely related to the more northerly *K. boliviana* and perhaps to *K. pennellii*. *Kallstroemia boliviana* differs in its perennial habit, hirsute and sericeous stems, obovate leaflets, usually two to three pairs of sericeous leaflets, yellow to orange flowers 2–3 cm in diameter, globose anthers, and strigose fruits. *Kallstroemia pennellii* has strigose stems, three to four pairs of leaflets, fruiting peduncles about 8 cm long, sericeous sepals 15 mm long, longer than the beak in fruit, yellow petals 3 cm long, strigillose fruits, and the mericarps abaxially cross-ridged and slightly keeled.

12. **Kallstroemia pennellii** D. M. Porter, *sp. nov.*

TYPE: Peru, Cajamarca: along Río Marañon, above Balsas, Amazonas, river bank, west shore, elev. 700–900 m; herb, petals yellow (lemon-chrome), 15 April 1948, *Francis W. Pennell 15185* (PH, holotype). This species is named for Francis Whittier Pennell (1886–1952), longtime Curator of Plants at the Academy of National Sciences of Philadelphia and collector of the type specimen.

Annua; caules ad 3 dm longi vel longiores, strigosi, trichomata antrorsa, alba, deinde glabrati; stipulae 4–5 mm longae, ca. 1 mm latae; folia elliptica, 2–4 cm longa, ca. 2 cm lata; foliolorum pares 3–4, late elliptica vel ovata, sericea, 9–14 mm longa, 3–6 mm lata, pares in medio laminae maxima; pedunculi quam folia subtendentia longiores, ad apicuem incrassati, in fructu recti et ca. 8 cm longi; sepala ovata, 15 mm longa, 3–4 mm lata, quam petala 1/2 breviora, sericea, marginea scarosi non involuti, ad anthesin quam stylus longiora, persistentia; petala lutea, 3 cm longa, ad apicem irregulariter erosa, marcescentia; stamina et stylus aequilongus; stylus ca. 10 mm longus; stigma oblongum, 2 mm longum; fructus ovoideus, 5 mm altus, 6 mm latus,

strigillosus; rostrum 8 mm longum, cylindricum, ad basin conicum, glabrum; mericarpia 5 mm alta, abaxialiter rugosa et subcarinata.

Annual; *stems* to 3 dm long or longer, strigose with white apically-directed trichomes, becoming glabrate; *stipules* 4–5 mm long, ca. 1 mm wide; *leaves* elliptical, 2–4 cm long, to ca. 2 cm wide; *leaflets* 3–4 pairs, broadly elliptical to ovate, sericeous, 9–14 mm long, 3–6 mm wide, middle pairs largest; *peduncles* longer than subtending leaves, thickened distally, straight and ca. 8 cm long in fruit; *sepals* ovate, 15 mm long, 3–4 mm wide, 1/2 as long as petals, sericeous, scarious margins not becoming involute, longer than style in flower, persistent; *petals* yellow, 3 cm long, apex irregularly notched, marcescent; *stamens* as long as style; *style* ca. 10 mm long; *stigma* oblong, 2 mm long; *fruit* ovoid, 5 mm high, 6 mm wide, strigillose; *beak* 8 mm long, cylindrical, base conical, glabrous; *mericarps* 5 mm high, abaxially cross-ridged and slightly keeled. *Fig. 12a, 12b. Map* 5.

FLOWERING DATES. Known to flower in April.

DISTRIBUTION AND HABITAT. Know only from the type locality *(Map 5).*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia pennellii* is characterized by its strigose stems, elliptical leaves, three to four pairs of sericeous leaflets, fruiting peduncles about 8 cm long, sericeous sepals 15 mm long, longer than the beak in fruit, the scarious margins not becoming involute, yellow petals 3 cm long, strigillose fruit, the beak glabrous and longer than the fruit body, and the cross-ridged and slightly keeled mericarps.

RELATIONSHIPS. *Kallstroemia pennellii* perhaps is most closely related to the more southerly *K. boliviana* and *K. tribuloides*. *Kallstroemia boliviana* differs by its hirsute and sericeous stems, obovate leaves, usually two to three pairs of leaflets, fruiting peduncles to about 4 cm long, hirsute and strigose sepals 6–9 mm long and shorter than the beak in fruit, yellow petals 12–19 mm long, strigose fruit, and abaxially rugose mericarps with flattened margins. *Kallstroemia tribuloides* has densely sericeous stems, three to six pairs of appressed-hirsute and sericeous leaflets, occasionally hexamerous orange flowers 1½–2½ cm in diameter, broadly ovate hirsute and strigose sepals shorter than the beak in fruit, glabrous fruit, and abaxially rugose mericarps with flattened and slightly keeled margins.

13. **Kallstroemia grandiflora** Torr. ex Gray, Pl. Wright. 1:28. 1852

TYPE: Arizona, Graham Co.: "Borders of the Gila," 28 October 1846, *Major Emory s. n.* (NY, lectotype). The label on Emory's specimen lists only the date, giving no locality data. Gray cited two collections following his description of *K. grandiflora,* "Borders of the Gila, *Col. Emory.*" and "Sonora Alta, Mexico, *Coulter,* No. 783." According to Emory's journal (Emory,

1848), on this date he was in what is now Graham County, Arizona, and collected along and near the Gila River. This specimen undoubtedly is the syntype cited by Gray. It was indirectly selected as the lectotype by Rydberg (in Vail & Rydberg, 1910, p. 114), who wrote "Type locality: Borders of the Gila River, Arizona." Notwithstanding Gray's citation of the authorship of this species (cf., Gray, 1853) as "Kallstroemia grandiflora, *Torr. in Pl. Wright.*", the correct citation undoubtedly is "Torr. ex Gray" rather than "Torr. in Gray," although Torrey himself used the latter (cf., Torrey, 1859). The original publication reads "Kallstroemia grandiflora *(Torr. in herb. Hook.),*" which leads one to conclude that this was a name taken by Gray from an annotation by Torrey on a specimen in W. J. Hooker's herbarium, rather than a name and description provided by Torrey. Further evidence is provided by Gray's original comment that, "Orders or genera elaborated by Dr. Engelmann, Dr. Torrey, Mr. Bentham, or others have the name of the author prefixed." In no other case that I can discover is a species published by another author in those sections of the publication authored by Gray. Gray probably came upon this name on his visit to Scotland in 1838–1839; Torrey had previously visited Hooker's Glasgow herbarium in 1833 (Rogers, 1942; Dupree, 1959).

Kallstroemia grandiflora var. *detonsa* Gray, *op. cit.* 1852. TYPE: Texas, "Near El Paso?" Sept. 1849, *Charles Wright 75* (GH, holotype; NY, holotype photograph; GH, isotype).

Tribulus grandiflorus (Torr. ex Gray) Brew. & Wats. in Brew., Wats. & Gray, Bot. Calif. 1:91. 1876. Brewer and Watson erroneously attributed this combination to Bentham and Hooker (1862). The latter authors never actually published it; they simply indicated that they considered *Kallstroemia* to be a subgenus of *Tribulus.*

Tribulus fisheri Kell., Proc. Calif. Acad. 7:162. 1877. TYPE: Mexico, Sonora: Agiabampo, 15 Sept. 1876, *Wm. J. Fisher s. n.* (UC, holotype).

Kallstroemia grandiflora var. *arizonica* Cockll., Bull. Torr. Bot. Club 27:87. 1900. TYPE: Arizona, Maricopa Co.: Phoenix, 9 Oct. 1899, *T. D. A. Cockerell s. n.* (Holotype presumably at COL, not seen; NY, US, isotypes).

Annual; *stems* decumbent to ascending, to over 1 m long and ca. 1 m high, densely sericeous with white and hispid with white or yellow apically-directed trichomes, rarely becoming glabrate; *stipules* 4–10 mm long, 1–2 mm wide; *leaves* elliptical, 1.5–7 cm long, 2–3 cm wide; *leaflets* 4–8(–10) pairs, elliptical to slightly obovate, appressed-hirsute, veins and margins sericeous, becoming glabrate, 8–25 mm long, 2–5 mm wide, middle pairs largest; *peduncles* longer than subtending leaves, extending flowers well above herbage, slightly thickened distally, 3–10.5 cm long, sharply bent at base and straight above in fruit; *flowers* pentamerous, 2–6 cm in diameter; *sepals* lanceolate, 6–16 mm long, 1.5–2.5 mm wide, ca. 1/2 as long as petals, hispid with much larger yellow or white and strigose with smaller white trichomes, in flower longer than style, in fruit much surpassing mature mericarps but shorter than beak, also shriveling and turning brown and margins becoming strongly involute making them appear linear, persistent; *petals* white through yellow to bright orange, base green to red and usually much brighter than distal portion, fading white to orange, broadly obovate, 10–34 mm long, 7–22 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid or oblong, rarely linear, 2–3 mm long, they and pollen red, orange, or rarely yellow, same color as petal base; *ovary* ovoid, 2–3 mm in diameter, pubescent; *style* 6–8 mm long, cylindrical, base slightly conical, strigose at base or to stigma base; *stigma* clavate, 2–3 mm long, 10-ridged, papillose; *fruit* ovoid, 4–5 mm in diameter, strigose; *beak* 6–18 mm long, ca. 3 times

length of fruit body, cylindrical, base conical, strigose at base or to stigma base; *mericarps* ca. 3.5 mm high and 1 mm wide, abaxially turbercled, sides slightly pitted, adaxial edge angled. *Fig. 13a, 13b. Map 14.*

FLOWERING DATES. In the north flowering mainly from June through October after the summer rains, and in the southwest (Jalisco to Guerrero) from August to March.

DISTRIBUTION AND HABITAT. Common in flat sandy areas throughout the Sonoran (except for Baja California) and Chihuahuan deserts from sea level to about 2000 meters; continuing southward through the semiarid lowland formations from Sinaloa to northern Guerrero and sparingly northward in Arizona *(Map 14).* In the north sympatric over much of its range with *Kallstroemia californica, K. hirsutissima, K. parviflora,* and *K. perennans,* and in the southwest overlapping with *K. hintonii, K. maxima, K. pubescens,* and *K. rosei.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia grandiflora* is easily recognized by its combination of decumbent to ascending stems, elliptical leaves, four to ten pairs of leaflets, fruiting peduncles longer than the subtending leaves and extending the flowers well above the herbage, white to bright orange flowers (the petal bases from green to red) 2–6 cm in diameter, lanceolate hispid and strigose sepals that much surpass the mature mericarps but are shorter than the beak, shriveling and turning brown and the margins becoming strongly involute making them appear linear, cylindrical style about three times as long as the ovary, clavate ten-ridged stigma, and strigose fruit with the beak about three times as long as the fruit body. *Kallstroemia parviflora* and *K. perennans* are the only species from the same area with which *K. grandiflora* is likely to be confused. *Kallstroemia parviflora* differs in its having three to six pairs of leaflets, fruiting peduncles 1–4 cm long, orange flowers 1–2½ cm in diameter, the anthers less than 1 mm in diameter, always yellow anthers and pollen, and oblong ten-ridged stigma; only depauperate individuals of *K. grandiflora* will be confused with this species. *Kallstroemia perennans* differs in having a perennial habit, densely hispid and strigose stems 1–2 cm long, four to five pairs of densely pubescent leaflets, fruiting peduncles shorter than the subtending leaves, fugaceous but not marcescent orange petals, the stamens only two-thirds as long as the style, oblong ten-ridged coarsely canescent stigma extending along the upper one-third of the

style, broadly ovoid hispid and strigose fruits 5–6 mm high and 8–10 wide, the beak hirsute at the base, and the mericarps abaxially cross-ridged and more or less keeled and 2½ mm wide.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. CALIFORNIA. Riverside Co.: Chuckawalla Valley near Desert Center, open ground near roadside, sandy soil, 900 ft, *Clary 2736* (POM). ARIZONA. Coconino Co.: Bill Williams Mt., *Anderson,* July 1864 (MO). Navajo Co.: McNary-Globe road near White River, *Gunning 3183* (ARIZ). Yavapai Co.: Beaver Creek, *Rusby,* Aug 1883 (F, MICH, NY, PH, US); 20 mi above Camp Verde, 4100 ft, *Wolf 2431* (CAS, DS, GH, RSA); Verde Valley, *W. W. Jones 80* (GH, UC), 25 July 1920 (POM, UC, US). Yuma Co.: dry arid hills around Ft. Yuma, *Schott,* 1 Dec 1854 (F); Mohawk, *M. E. Jones 24965* (POM). Maricopa Co.: 10 mi W of Aguila on US Highway 70, roadside, *J. D. Porter,* 30 Aug 1962 (GH); Sentinal, *M. E. Jones 24962* (CAS, GH, MO, NY, POM, UC). Gila Co.: near Globe, *Peebles, Harrison & Kearney 4391* (ARIZ, US); mesa near Rock & Rye Creeks, 990–1050 m, *Collom 187* (GH, MICH, MO, NY, US); San Carlos, 2500 ft, *Rothrock 777* (F, GH, RSA, US). Pinal Co.: desert mesa near Apache Junction, *Gillespie 8442* (DS, GH, UC, US); Oracle, 4500 ft, *Thornber,* 9–13 Sept 1905 (ARIZ, UC); Sacaton, *Gilman s. n.* (MO), *271* (DS, MO), *283* (CAS). Graham Co.: Camp Grant, 4753 ft, *Rothrock 442* (CAS, DS, F, NY); Galluro Mts., *Toumey,* 29 July 1894 (ARIZ, GH), *275* (UC). Greenlee Co.: Clifton, *Davidson 14* (UC), *758* (DS). Pima Co.: flats below Baboquivari Canyon, *Gilman 22* (DS, F, MO, NY); Continental, *Shreve 6600* (ARIZ, DS, MICH); Tucson, 2400 ft, *Thornber 263* (ARIZ, DS, MO, NY, POM, UC). Santa Cruz Co.: Nogales, *M. E. Jones 22312* (F, MO, POM); near Ruby, ca. 1375 m, *Morton 10* (POM). Cochise Co.: Apache Pass, *Lemmon,* Sept 1881 in part (BM, F, UC); Cave Creek Canyon, *Kusche,* 24–26 Aug 1927 (CAS, F, POM); San Bernardino Ranch, *Mearns 612* (DS, US). NEW MEXICO. Bernalillo Co.: Albuquerque, *M. E. Jones 4121* (POM). Grant Co.: Mangas Springs, 4770 ft, *Metcalfe 624* (ARIZ, BM, GH, MO, NY, UC, US); valley below Ojo de Gavilán, *Wright 911* (BM, GH, MO, NY, PH, US). Chaves Co.: Bottomless Lakes, sandy soil, *Stiteler,* 20 June 1949 (PH). Hidalgo Co.: Separ, sandy soil, 4300 ft, *Benson 7384* (POM). Luna Co.: near Akela, *Schallert 21174* (SMU); Florida Mts., *Mulford 1073* (MO, NY). Dona Ana Co.: along Rio Grande near Ft. Selden, *Rusby 56* (F, MICH, MO, NY, PH); Rio Grande Valley below Dona Ana, *Parry, et al. 139* (NY, PH, US). TEXAS. El Paso Co.: El Paso, alluvial hills, 1000 m, *Fosberg S3898* (GH, LL, NY, SMU); Franklin Mts., limestone soil, 4300 ft, *Warnock 8226* (LL, MICH, SMU, TEX). Hudspeth Co.: between Nulo and Harris Siding, *Ferris & Duncan 2447* (DS); 5 mi W of Van Horn, gravelly soil along highway, *Warnock 13619* (LL, TEX). Loving Co.: ca. 3 mi W of Mentone, limestone soil along highway, 2700 ft, *Warnock 10629* (LL, SMU). Jeff Davis Co.: 13.5 mi SW of Chispa, calcareous gravel, *Waterfall 5301* (GH, MO); Mt. Livermore, *Hinckley 8* (F, NY). Presidio Co.: dry creek beds near Chinati Mts., *Hinckley 818* (ARIZ, F, GH, NY, SMU, TEX); alluvial hills between Redford and Presidio, 3200 ft, *Warnock 10611* (LL, SMU). Brewster Co.: Big Bend Natl. Park, 6 mi N of Rio Grande, dry arroyo walls, 3000 ft, *Rollins & Chambers 2768* (DS, GH, UC, US); Boquillas, *Marsh 53* (GH, SMU, TEX); arroyos near Hot Springs, *Warnock,* 17 July 1937 (ARIZ, GH, TEX).

MEXICO. SONORA: Guaymas, hills and valleys, *Palmer 177* (BM, DS,

GH, NY, PH, UC, US), stony slopes, *225* (BM, GH, MICH, NY, US); llano 27 mi W of Hermosillo toward Kino Bay, *Wiggins & Rollins 129* (ARIZ, DS, GH, MICH, MO, NY); San Bernardo, mesas and milpas, *Gentry 1667* (ARIZ, F, GH, MEXU, MO, NY, UC, US). CHIHUAHUA: Bachimba, roadside, *Knobloch 294* (BM, LL, MSC); El Carmen, *LeSueur 381* (F, GH, MO, SMU, TEX, UC); Hacienda San Miguel, near Batopilas, *Palmer 108* (BM, CAS, GH, MICH, NY, PH, US). COAHUILA: 2 km NE of Las Delicias, caliche slopes, *Stewart 2958* (GH); dry valley between La Vibora and Matrimonio Viejo, gypsum beds, *Johnston 9338* (GH). SINALOA: Imala, *Palmer 1440* (F, GH, NY, US); low hills 8 mi N of Mazatlán, *Waterfall 12751* (ARIZ, GH, MICH, RSA, TEX, UC); Rosario, *Lamb 471* (DS, GH, MICH, MO, MSC, NY, US). DURANGO: base of hills 2 mi W of Bermejillo toward Palmito Dam, silty soil, *Johnston 7749* (GH); 27 mi NE of Cuencame toward Torreón, desert scrub, among rocks, 6300 ft, *Straw & Forman 1520* (MICH, RSA). NAYARIT: Acaponeta, *Lamb 530* (GH, MO, MSC, NY, US), *534* (DS, GH, MSC, NY, US); Cañon de Jesús María, bottom lands along Río Jesús María, 1000 ft, *Goldsmith 141* (F, GH, MO, UC, US). JALISCO: between La Venta and Ixtlán, 1100 m, *Reko 4491* (US). COLIMA: Colima, *Palmer 83* (ARIZ, MICH, UC, US), *1110* (BM, GH, MICH, NY, US); Manzanillo, *Xantus,* 1863 (F, GH, NY, US); 5 km W of Tecomán, fine silt at roadside, *Porter 1482* (GH, MEXU). MICHOACAN: Tacupa, bank of Río Balsas, on sand, *Hinton 5487* (BM, GH, MO, NY, US), *7116* (ARIZ, BM, F, GH, LL, NY, PH, RSA, TEX, US). GUERRERO: Pungarabato, bank of Río Cutzamala, *Hinton 6480* (F, GH, MICH, NY, US).

A specimen at PH labeled "Moore's Flat, Sierra Nevada, Nevada Co., Cal. July 1867." could not have been collected in this locality, far from the range of any species of *Kallstroemia*. It is a mixed collection of *K. grandiflora* and *Tribulus cistoides* and possibly may be from western Mexico, where both of these species do occur. *Schott 1* from F, labeled "Cartejena [Colombia], beach.", was undoubtedly switched with a specimen of *T. cistoides*, which occurs in that locality. This collection of *K. grandiflora* probably is from Arizona, where Schott also collected.

COMMON NAMES. Like many other plants with conspicuous flowers, *Kallstroemia grandiflora* is graced with a number of common names. However, surprisingly, it is not known by nearly as many names as is the much less conspicuously flowered *K. maxima*. This undoubtedly is due to the latter's wide use in the native *materia medica*, while the former is utilized, if at all, only as an ornamental. Common names that have been reported for *K. grandiflora* are Abrojo de Flor Amarillo (Chihuahua, Durango); Arizona Poppy (Arizona); Baiburín (Sinaloa, Sonora); Desert Poppy (Texas); Mal de Ojos (Sonora); Manrubio (Colima); Mexican Poppy, Ojo Mal, Poppy (Arizona); San Miguelito (Sonora); and Summer Poppy (Arizona). Prevalence of the word "poppy" as part of the common name in much of the southwestern United States reflects the superficial resemblance of the flowers in size and color to the California Poppy, *Eschscholzia*

californica Cham. *(Papaveraceae)*, commonly grown in the same area as an ornamental.

VARIATION. Variation in the color of trichomes on the vegetative parts of the plants is sometimes quite striking. If the larger, hispid trichomes are yellow, as is normally the case, individuals have a decided yellowish cast. If these trichomes are white, the plants appear gray. Specimens from the Sonoran Desert and its environs tend to be yellow, and those from the Chihuahuan Desert tend to be gray, but this criterion is too variable to be utilized in the recognition of subspecific entities.

Flower color in *Kallstroemia grandiflora* is rather variable, but that of individual populations appears to be remarkably stable. It ranges from yellow to distally orange with a dark orange basal spot, or dark orange with a red basal spot. Occasional populations are found in which the petals are white with a red basal spot. There appears to be genetic linkage between the color of the petal base and filament, anther, and pollen color. All are the same in an individual. This color variation is not such that subspecific taxa can be recognized, in that it appears to have no ecological or geographical correlation.

RELATIONSHIPS. *Kallstroemia grandiflora* appears to be the center of a group of interrelated species also involving *K. parviflora*, *K. peninsularis*, and *K. perennans*. The characters distinguishing *K. parviflora* and *K. perennans* from *K. grandiflora* are summarized above. *Kallstroemia peninsularis* differs in having hirsute and hirtellous stems with retrorse pubescence, two to five pairs of leaflets, yellow to orange flowers 1–3½ cm in diameter, hispid and hirtellous sepals, yellow anthers and pollen, and a clavate stigma that extends along the upper one-third to almost the entire length of the style.

14. **Kallstroemia peninsularis** D. M. Porter, *sp. nov.*

TYPE: Mexico, Baja California Sur: granitic hills 10 mi SE of La Paz on road to Los Planes, elev. 725 ft; petals golden yellow, 1 December 1959, *Ira L. Wiggins 15686* (GH, holotype; DS, GH, TEX, isotypes).

Annua; caules prostrati vel decumbentes, decimetra aliquot longi, albi- vel lutei-hirsuti et hirtelli, trichomata retrorsa; stipulae 2–4 mm longae, 1–2 mm latae; folia elliptica, 1.5–6.5 cm longa, 2–4 cm lata; foliolorum pares 2–5, foliola elliptica vel oblonga, appresse hirsuta, margines venaeque sericeae, 8–34 mm longa, 3–17 mm lata, pares in medio laminae maxima; pedunculi quam folia subtendentia longiores vel breviores, ad apicem incrassati, anthesin 10–52 mm longi, in fructu 19–64 mm longi, ad basin acute flexi et sursum recti; flores pentameri, 1–3.5 cm in diametro; sepala subulata, 5–8

mm longa, 1–2 mm lata, quam petala 1/2–1/3 breviora, lutei-hispida et albi-hirtella, ad anthesin quam stylus longiora, in fructu mericarpia matura multo excedentia sed quam rostrum breviora, margines deinde perinvoluti et quasi-linearia, persistentia; petala lutea vel aurantiaca, late obovata, ad apicem late rotundata vel irregulariter erosa, 11–20 mm longa, 7–15 mm lata, marcescentia; stamina et stylus aequilongus; antherae ovoideae, 1–2 mm in diametro, antherae et pollen luteum; ovarium ovoideum, 1–3 mm in diametro, pubescens; stylus 3–8 mm longus, anguste cylindricus, ad basin leviter conicus, ad basin stigmatis strigosus; stigma clavatum, stylum in longitudine subaequans vel 2/3 brevius, 10-porcatum, papillosum; fructus ovoideus, 3.5–5 mm in diametro, strigillosus; rostrum 7–10 mm longum, cylindricum, ad basin conicum, ad stigmatam strigosum; mericarpia 3–4 mm alta, ca. 1 mm lata, abaxialiter rotundato-tuberculata, latera foveolata, adaxialiter subangulata.

Annual; *stems* prostrate to decumbent, to several dm long, hirsute with white or yellow and hirtellous with white retrorse trichomes; *stipules* 2–4 mm long, 1–2 mm wide; *leaves* elliptical, 1.5–6.5 cm long, 2–4 cm wide; *leaflets* 2–5 pairs, elliptical to oblong, appressed-hirsute, veins and margins sericeous, 8–34 mm long, 3–17 mm wide, middle pairs largest; *peduncles* longer or shorter than subtending leaves, thickened distally, 10–52 mm long in flower, 19–64 mm long in fruit and bent sharply at base and straight above; *flowers* pentamerous, 1–3.5 cm in diameter; *sepals* subulate, 5–8 mm long, 1–2 mm wide, 1/3–1/2 as long as petals, hispid with yellow and hirtellous with white trichomes, longer than style in flower, in fruit much exceeding mature mericarps but shorter than beak, shriveling and margins becoming strongly involute making them appear almost linear, persistent; *petals* yellow to orange, broadly obovate, apex broadly rounded to irregularly notched, 11–20 mm long, 7–15 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid, 1–2 mm in diameter, they and pollen yellow; *ovary* ovoid, 1–3 mm in diameter, pubescent; *style* 3–8 mm long, narrowly cylindrical, base slightly conical, strigose to stigma base; *stigma* clavate, extending along upper 1/3 to ca. entire length of style, 10-ridged, papillose; *fruit* ovoid, 3.5–5 mm in diameter, strigillose; *beak* 7–10 mm long, cylindrical, base conical, strigose to stigma base; *mericarps* 3–4 mm high, ca. 1 mm wide, abaxially with rounded tubercles, sides pitted, adaxial edge slightly angled. *Fig. 14a, 14b. Map 15.*

FLOWERING DATES. August through March, following both summer and winter rains.

DISTRIBUTION AND HABITAT. Endemic to the southern part of the territory of Baja California, Mexico *(Map 15)*. Found mainly in low sandy areas and sand dunes near beaches from sea level to perhaps 1000 meters or higher. *Kallstroemia californica* also extends into this area.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia peninsularis* is easily recognized by its combination of hirsute and hirtellous stems with retrorse trichomes, elliptical leaves, two to five pairs of leaflets, yellow to orange flowers 1–3½ cm in diameter, hispid and hirtellous sepals which are longer than the mature mericarps but shorter than the beak, shriveling and the margins becoming

strongly involute and making them appear almost linear, yellow anthers and pollen, narrowly cylindrical style about three times as long as the ovary, a clavate stigma extending along the upper one-third to almost the entire length of the style, and strigillose fruit with the beak about three times as long as the fruit body.

SPECIMENS EXAMINED. MEXICO. BAJA CALIFORNIA: Arroyo Salado, *Purpus 409* (UC); near Arroyo Salado, margin of ocean sand dunes, *Hammerly 189* (CAS, DS); Cabo San Lucas, *Xantus 14* (GH, NY, US); 3 km N of Cabo San Lucas, flat area, *Moran 7040* (DS); 14.4 km SW of Comondú, steep slope in canyon, *Carter, Alexander & Kellogg 2122* (DS, US); 0.5 mi W of SW base of Los Frailes, sandy dunes, *Porter 318* (CAS, DS); arroyo 95 km NW of La Paz, 75 m, *Wiggins 15413* (CAS, DS, UC); highway NW of La Paz near km 40, *Thomas 8439* (CAS, DS, GH, US); 24 mi W of La Paz, rocky sand at roadside, *Porter 438* (DS); ca. 15 mi W of La Paz, coarse granitic sand on bluff, *Hammerly 222* (CAS, DS, US); gulch in granitic hills 15.5 mi SE of La Paz toward Las Cruces, 570 ft, *Wiggins 15669A* (DS); near junction of roads to Punta Arenas and Bahía de los Muertos, rocky hillside, *Wiggins 14454* (CAS, DS, MICH); wash 1 mi S of San Antonio toward Santiago, *Chambers 860* (DS, UC); San José del Cabo, *Brandegee 78* (UC), 5 Sept 1891 (DS), 12 Sept 1891 (F), *M. E. Jones 27114* (POM); 3 mi NE of San Lucas, sandy red soil at roadside, *Porter 331* (CAS, DS); 14 mi N of San Lucas, sandy decomposed granite in road, *Porter 341* (DS); 12.8 km N of Santiago, granitic sand, *Carter, Alexander & Kellogg 2181* (DS, US).

COMMON NAME. Patagallina.

TAXONOMY. In a previous publication (Porter, 1963), this taxon was confused with *Kallstroemia grandiflora* and *K. pubescens*. However, a more adequate knowledge of the genus has revealed that it is a new species.

RELATIONSHIPS. *Kallstroemia peninsularis* is most closely related to *K. grandiflora*. The latter differs in having densely sericeous and hirsute decumbent to ascending stems, four to ten pairs of leaflets, fruiting peduncles 3–10½ cm long that extend the flowers well above the herbage, the flowers from 2–6 cm in diameter, hispid and strigose sepals, the petals basally darker in color than the distal portion, the anthers and pollen rarely yellow, a clavate ten-ridged stigma less than one-third as long as the style, and strigose fruits.

15. **Kallstroemia perennans** Turner, Field & Lab. **18**:155. 1950

TYPE: Texas, Val Verde Co.: Langtry, May 1913, *C. R. Orcutt 6126* (MO, holotype; GH, MO, holotype photographs). Based on *Kallstroemia hirsuta* L. Williams, Ann. Mo. Bot. Gard. **22**:49. 1935. Not *K. hirsuta* (Benth.) Engl.

in Engl. & Prantl, Nat. Pflanzenfam. 3(4):88. 1890 [=*Tribulus hirsutus* Benth., Fl. Austral. 1:289. 1863].

Perennial; *stems* prostrate to ascending, 1–2 dm long, densely hispid with bulbous-based white or yellow and strigose with white apically-directed trichomes; *stipules* 3–5 mm long, 1–1.5 mm wide; *leaves* elliptical, 2–5.5 cm long, 2–3 cm wide, densely pubescent; *leaflets* 4–5 pairs, oblong to ovate, densely appressed-hirsute, veins and margins sericeous, 13–18 mm long, 6–10 mm wide, middle pairs largest; *peduncles* shorter than subtending leaves, little thickened distally, 15–20 mm long in flower, 25–36 mm long in fruit and bent sharply at base and straight above; *flowers* pentamerous, 3.5–4.5 cm in diameter; *sepals* lanceolate, 13–15 mm long, 1.5–2.5 mm wide, ca. 1/2 as long as petals, densely hispid and strigose, longer than style in flower, spreading from base of mature fruit and longer than mericarps but shorter than beak, margins becoming sharply involute, persistent; *petals* orange, obovate, 19–26 mm long, 10 mm wide, fugaceous but not marcescent; *stamens* 2/3 as long as style; *anthers* ovoid, 1.5 mm in diameter, they and pollen orange; *ovary* ovoid, 3 mm in diameter, pubescent; *style* 6 mm long, cylindrical; *stigma* oblong, 10-ridged, 2–3 mm long, coarsely canescent; *fruit* broadly ovoid, 5–6 mm high, 8–10 mm wide, hispid and strigose, hispid trichomes to 5 mm long; *beak* 6–10 mm long, cylindrical, base hirsute and slightly conical; *mericarps* 4 mm high, 2.5 mm wide, abaxially cross-ridged and more or less keeled, sides pitted, adaxial edge straight. *Fig. 15a, 15b. Map 15.*

FLOWERING DATES. May through August, following the spring and summer rains.

DISTRIBUTION AND HABITAT. The Chihuahuan Desert; known only from southern Presidio, Brewster, and Val Verde counties, Texas *(Map 15)*, where apparently confined to limestone soils. Sympatric with *Kallstroemia californica, K. grandiflora, K. hirsutissima,* and *K. parviflora.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia perennans* may be easily recognized by its having a combination of perennial habit, short prostrate to ascending stems, elliptical leaves, four to five densely pubescent leaflets, fruiting peduncles shorter than the subtending leaves, densely hispid and strigose sepals that spread from the base of the mature fruit and curve upward surpassing the mature mericarps but shorter than the beak, margins becoming sharply involute, orange petals that are fugaceous but not marcescent, stamens two-thirds as long as the style, a cylindrical style about twice as long as the ovary, oblong ten-ridged coarsely canescent stigma that extends about one-third the length of the style, broadly ovoid hispid and strigose fruit from 5–6 mm high and 8–10 wide, cylindrical beak about twice as long as the fruit body, and abaxially cross-ridged and more or less keeled mericarps 2½ mm wide. The only species from the same

area with which *Kallstroemia perennans* might be confused is *K. grandiflora.* The latter differs from *K. perennans* in its annual habit, decumbent to ascending stems reaching to over 1 m in length, four to ten pairs of leaflets, fruiting peduncles longer than the subtending leaves, sepals shriveling and turning brown, the margins becoming strongly involute and making them appear linear, fugaceous and marcescent yellow to bright orange petals with usually a darker base, the stamens as long as the style, clavate ten-ridged papillose stigma, ovoid strigose fruit, and abaxially tubercled mericarps about 1 mm wide.

SPECIMENS EXAMINED. UNITED STATES. TEXAS. Locality unknown: Rio Colorado, *V. Havard,* 1883 (F). Presidio Co.: limestone hills between Lajitas and Arroyo Segunda, 2215 ft, *Warnock & Turner 1350* (LL). Brewster Co.: Amarilla Mt., 7 mi W of Terlingua, 2640 ft, *Turner 1166* (GH); W of Lajitas toward Fresno Canyon, limestone soil, 3200 ft, *Turner & Parks 1350* (SMU). Val Verde Co.: rocky calcareous hillside 3.5 mi W of Langtry, *Turner 3779* (RSA, SMU, TEX); limestone hills 19 mi N of Langtry, *McVaugh 8226A* (GH, MICH).

RELATIONSHIPS. Williams *(loc. cit.)* was the first to indicate that *Kallstroemia perennans* is most closely allied to *K. grandiflora.* The differences between these two species are reviewed above.

16. **Kallstroemia parviflora** Norton, Ann. Rept. Mo. Bot. Gard. 9:153. 1898

TYPE: Texas, Bexar Co.: San Antonio, 1897, *E. H. Wilkinson 184* (MO, lectotype). Notwithstanding Rydberg's (in Vail & Rydberg, 1910) indirect citation of *Pollard 1295* as the type collection of this species by listing "Agricultural College, Mississippi" for the type locality, Wilkinson's specimen is the type. Both collections were cited by Norton in his description of the species, and the Wilkinson specimen at MO bears the word "Type," presumably in Norton's handwriting. It is confirmed as the lectotype.

Kallstroemia intermedia Rydb. in Vail & Rydb., N. Amer. Fl. **25**:113. 1910. TYPE: Texas, Bexar Co.: 1904. *Gust. Jermy s. n.* (NY, holotype; UC, holotype fragment).

Kallstroemia laetevirens Thornb. in Woot. & Standl., Contr. U. S. Nat. Herb. **16**:143. 1913: TYPE: New Mexico, Grant Co.: Hanover Mountain, 31 July 1911, *J. M. Holzinger s. n.* (US, holotype; MO, isotype?).

Annual; *stems* prostrate to decumbent or ascending, to 1 m or more long, more or less coarsely hirsute and sericeous with apically-directed white or gray trichomes, becoming glabrate; *stipules* 5–7 mm long, 1–3 mm wide; *leaves* elliptical, 1–6 cm long, to 3 cm wide; *leaflets* 3–5(–6) pairs, elliptical to oblong or oval, appressed-hirsute, veins and margins sericeous, 8–19 mm long, 3.5–9 mm wide, middle pairs largest; *peduncles* equalling or commonly longer than subtending leaves, thickened distally, 1–4 cm long in flower and fruit, in fruit straight or sharply bent at base and straight above; *flowers*

pentamerous, 1–2.5 cm in diameter; *sepals* lanceolate, 4–7 mm long, 1–2 mm wide, hispid with white or rarely yellow and strigose with white trichomes, in flower longer than style, in fruit shriveling and turning brown, appressed to mericarps and reaching from top of mericarps to ca. as long as style, margins becoming sharply involute, persistent; *petals* orange, drying white to yellow, narrowly obovate, 5–11 mm long, 3.5–6 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid, rarely linear, less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, pubescent, ca. 1 mm in diameter; *style* as long or longer than ovary, cylindrical, strigose to glabrous; *stigma* oblong, 10-ridged, ca. 1 mm long, papillose; *fruit* ovoid, 3–4 mm high, 4–6 mm wide, strigose; *beak* 3–9 mm long, as long as to 3 times fruit body, strigose to glabrous, trichomes appressed to spreading, cylindrical, base scarcely conical; *mericarps* 3–4 mm high, ca. 1 mm wide, abaxially rugose to tubercled, sides lightly to strongly pitted, adaxial edge angled. *Fig. 16a, 16b. Maps 5, 16.*

FLOWERING DATES. Seed germination, plant growth, and flowering take place mainly after summer rains. These phenomena usually occur from July through September in North America, and from November to April in Peru.

DISTRIBUTION AND HABITAT. Disturbed areas mainly in various grassland associations from Colorado and Kansas south to Guanajuato, Querétaro, and Hidalgo, Mexico, and west to Arizona, occurring sparingly in the Chihuahuan Desert, extending as a weed in all directions; introduced into western and central Peru *(Maps 5 and 16)*. Found from about 100 to 2600 m in North America and 1300 to 2850 m in Peru. Sympatric with *Kallstroemia californica, K. grandiflora, K. hirsutissima,* and *K. perennans* in the north, *K. rosei* in the south, and barely overlapping with *K. maxima* in the southeast.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia parviflora* is distinguished by its combination of elliptical leaves, three to six pairs of leaflets, fruiting peduncles 1–4 cm long, orange flowers 1–2½ cm in diameter, hispid and strigose sepals longer than the mature mericarps but shorter than the beak, shriveling and turning brown and the margins becoming strongly involute, yellow anthers and pollen, cylindrical style as long or longer than the ovary, oblong ten-ridged stigma, cylindrical beak as long to three times as long as the strigose fruit body, and abaxially rugose to tubercled mericarps. Depauperate specimens of *K. parviflora* may be confused with *K. californica,* and more robust specimens with *K. grandiflora. Kallstroemia californica* differs in having hirsute and strigose stems, three to seven pairs of leaflets, fruiting peduncles shorter than the subtending leaves, yellow flowers 1 cm

or less in diameter, usually deciduous sepals, a stout conical style shorter than the ovary, a clavate ten-ridged stigma, strigillose fruit with the beak shorter than the fruit body, and mericarps with four or five blunt oblong tubercles that may be 1½ mm long. *Kallstroemia grandiflora* has four to ten pairs of leaflets, fruiting peduncles 3–10½ cm long, white to bright orange flowers (petal bases darker than the distal portion) 2–6 cm in diameter, anthers 2–3 mm long, usually orange or red anthers and pollen, style about three times as long as the ovary, and clavate ten-ridged stigma.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. CALIFORNIA. San Bernardino Co.: Coliseum Mine, Clark Mts., dry sandy exposed south slope, *Roos & Roos 4904* (CAS, DS, NY, RSA, UC). San Diego Co.: Warner Hot Springs, *Gander 2944* (POM). NEVADA. Clark Co.: Nelson, 3400 ft, *Low BL-8* (UC). UTAH. Without locality: *Bishop*, 1874 (POM). COLORADO. Boulder Co.: Boulder, *Pammel*, 25 Aug 1913 (TEX). Fremont Co.: Oil Creek, *Brandegee 705* (MO, NY, PH, UC). Pueblo Co.: Pueblo, along railroad track near depot, *Baker, Earle & Tracy 4* (BM, F, GH, MICH, MO, NY, POM, UC, US). Otero Co.: La Junta, 6000–7000 ft, *Beckwith 89* (NY). Bent Co.: Caddoa, Wooton, 13 Sept 1897 (US). Las Animas Co.: near Troy, *Rogers 5396* (MICH, TEX, US). Baca Co.: breaks of East Carrizo Creek 5 mi SW of Kirkwell, 4700 ft, *Weber 5102* (RSA, UC). KANSAS. Rooks Co.: Stockton, low prairie, *Runyon 231* (ARIZ). Wyandotte Co.: Wyandotte, railway yards, *Mackenzie*, 16 Aug 1896 (NY). Wallace Co.: Ft. Wallace, *Bell*, 1867 (PH). Logan Co.: without locality, cultivated soil, *Hitchcock 53* (GH, MO, NY, US). Russell Co.: bluff along Saline River 5 mi N of Russell, barren banks, *McGregor 12675* (US). Barton Co.: Chaflin, *Benke 2437* (F). Anderson Co.: Garnett, *Carlton 362* (ARIZ, US). Hamilton Co.: Coolidge, dry hills, *Smyth 216* (NY, US). Kearney Co.: Deerfield, along A.T.&S.F. railroad, *Blake 978* (LL, US). Ford Co.: without locality, *Eggert*, 24 Aug 1902 (MO). Sedgewick Co.: Wichita, along A.T.&S.F. railroad, *Bartley 1210* (NY, US). Meade Co.: Advance Flag Station, dry grassland, 2550 ft, *Horr 3436* (GH). MISSOURI. Jackson Co.: Kansas City, waste ground, *Bush 8168* (GH, MO, NY, US), *8168A* (CAS). St. Louis Co.: Allenton, *Letterman*, 1897 (MO). St. Louis City: St. Louis, railroad banks, *Eggert*, Aug 1883 (NY). ILLINOIS. Cook Co.: Chicago, *Moffatt 9507* (WIS). Macoupin Co.: along C.&A. railroad near Brighton, *Moffatt 498* (WIS). St. Clair Co.: East St. Louis, *Eggert*, 8 Aug 1897 (DS, F, MO, NY, TEX, UC, US). ARIZONA. Mohave Co.: Kingman, 3300 ft, *Kearney & Peebles 12594* (ARIZ, US). Coconino Co.: Havasupai Canyon, flat areas, *Clover 7007* (SMU). Navajo Co.: Holbrook, *Zuck*, 10 Aug 1896 (F, MO, NY, US). Apache Co.: Navajo Indian Reservation near N end of Carrizo Mts., dry hills, *Standley 7475* (US). Yavapai Co.: Prescott, *Peebles, Harrison & Kearney 8862* (ARIZ, F, POM). Gila Co.: mesa near Rock Creek, 1050 m, *Collom 322* (MICH, MO, US). Maricopa Co.: Agua Caliente, *Thornber 7286* (ARIZ, UC). Pinal Co.: San Tan Mts., *Peebles, Harrison & Kearney 145* (ARIZ). Greenlee Co.: Blue River, *Davidson 757* (DS, UC). Pima Co.: Stone Cabin Canyon, Santa Rita Mts., *Griffiths & Thornber 284* (ARIZ, NY, US). Santa Cruz Co.: 1 mi E of Canelo, desert grassland, *Benson 11494* (DS, POM). Cochise Co.: Paradise, under ditch, *Blumer 2272* (ARIZ, F,

US). NEW MEXICO. San Juan Co.: desert draw S of Shiprock, sand, *Waterfall 11730* (RSA, TEX, UC, US). Rio Arriba Co.: Chama River, *Wooton 2897* (US). Taos Co.: Ojo Caliente, 6000 ft, *B. H. Smith,* 25 Aug 1893 (PH). Colfax Co.: Raton, *Cockerell,* 29 Aug 1900 (NY). Santa Fe Co.: Santa Fe, 7200 ft, *Heller & Heller 3746* (BM, DS, GH, MSC, NY, US). San Miguel Co.: Las Vegas, 1900 m, *Bro. Arsene 16203* (BM, F). Quay Co.: Nara Visa, sand soil, *Fisher 72* (US). Bernalillo Co.: Albuquerque, *M. E. Jones 4121* in part (BM, CAS, DS, F, MSC, NY, PH, POM, UC, US). Guadalupe Co.: 1.5 mi ENE of Santa Rosa, sandy soil, *Shinners 21039* (SMU). Catron Co.: S of Bat Cave, 14 mi SW of Horse Springs, gravelly soil on canyon floor, *C. E. Smith 213* (ARIZ, PH). Socorro Co.: Socorro, *Vasey 69* (BM, F), July 1881 (F, US). Lincoln Co.: Gray, ca. 6000 ft, *Skehan 52* (F, GH, MO, NY, POM, UC). Chaves Co.: 20 mi S of Roswell, ca. 3600 ft, *Earle & Earle 307* in part (BM, MO, NY, POM, US). Grant Co.: Mangas Springs, 4770 ft, *Metcalfe 644* (ARIZ, BM, GH, MO, NY, UC, US). Sierra Co.: Kingston, ca. 6600 ft, *Metcalfe 1197* (ARIZ, CAS, MO, US). Hidalgo Co.: near Steins, sandy soils, 4000 ft. *Hershey 3441* (GH). Luna Co.: 3 mi E of Deming, sand dunes, *Shreve 8227* (ARIZ). Dona Ana Co.: Organ Mts., 4500 ft, *Wooton 423* (DS, MO, NY, POM, UC, US). Otero Co.: White Sands, *Wooton,* 24 Aug 1899 (US). Eddy Co.: near US Highway 62 3 mi N of Texas state line, grassy gypsum flat between gypsum hills, *Waterfall 5739* (GH, MO, NY). OKLAHOMA. Cimarron Co.: John Regnier Ranch, Kenton, *Demaree 13384* (GH, NY, SMU). Kay Co.: without locality, *M. White,* 28 July 1898 (NY). Major Co.: bare old road near Cleo. *Stevens 1747* (GH, NY). Payne Co.: Stillwater, *Brillhart 123* (TEX). Oklahoma Co.: prairie 2 mi N of Bethany, clay soil, *Waterfall 1693* (NY). Harmon Co.: abandoned field near Hollis, *Stevens 1119* (GH, POM). Jackson Co.: 3 mi SW of Atlas, clay loam soil, *Prater 81* (TEX). Kiowa Co.: bare roadside near Mountain Park, *Stevens 1236* (DS, GH, MO, US). Comanche Co.: Ft. Sill, *Clemens 11652* (CAS, GH, MO). Murray Co.: 5 mi S of Sulphur, roadside, *Waterfall 12293* (RSA, TEX). Marshall Co.: 3.5 mi W of Kingston, gravel-clay bed of Buncombe Creek, *Goodman 6918* (RSA, SMU, UC). Bryan Co.: near Durant, *Blain 86* (US). TEXAS. Randall Co.: Palo Duro Canyon State Park, Permian redbeds, *Correll & Johnston 17130* (LL). Hardeman Co.: 8 mi NW of Quanah, spots denuded of grass in heavily grazed pasture, *Cory 50127* (NY, SMU). Foard Co.: 6.8 mi S of Crowell, brown-red sandy clay on road shoulder, *Shinners 30792* (SMU). Crosby Co.: near Walker Tank, SW of Spur, green edge of dried-up stream, *Erlanson 1143, 1155* (MICH). Knox Co.: 1 mi E of Benjamin, sandy clay roadside, *Shinners 20794* (SMU). Clay Co.: 11.8 mi NW of Henrietta, red-brown sandy silt and gravel between highway and railroad, *Shinners 15227* (SMU). Grayson Co.: Denison, 725 ft, *Letterman 70* (F, MO, NY). Jack Co.: 10.5 mi ENE of Jacksboro, sandy clay road margin, *Shinners 19012* (SMU). Denton Co.: Denton, sandy loam, *McCart 8913* (TEX). Collin Co.: along railroad near Plano, *Lundell & Lundell 9307* (LL, MICH). Shackelford Co.: 0.4 mi W of S entrance to Ft. Griffin State Park, road shoulder, *Cory 58436* (SMU). Stephens Co.: roadside just W of Caddo, *Thieret 16177* (SMU). Tarrant Co.: near airfield E of Euless, open grounds along highway, *Whitehouse 16438* (MICH, NY, SMU, UC, US). Dallas Co.: Dallas, outcropping limestone, *Lundell 11571* (LL, US, TEX). Martin Co.: Stanton, sandy ground, *Eggert,* 13 June 1900 (MO). Howard Co.: Big Spring, *Tracy 8298* (BM, F, GH, MO, MSC, NY, TEX, US). Mitchell Co.: Colorado, dry sandy open ground, *E. J. Palmer 13773* (MO, US, WIS). Nolan Co.: near Blackwell, sandy soil, open ground, *E. J. Palmer 34590* (MO, NY, PH).

Taylor Co.: Camp Berkeley, disturbed rocky soil, *Tolstead 7688* (GH, LL, NY, SMU, TEX, UC). Eastland Co.: Ranger, *Robinson 49* (GH, TEX). Hood Co.: Granbury, *E. J. Palmer 6517* (F, MO, POM). Ellis Co.: 1 mi W of Ennis, dry sandy soil, *Shackelford 24* (SMU). Gregg Co.: without locality, *C. L. York,* summer 1941 (GH, TEX). Loving Co.: along highway ca. 3 mi W of Mentone, limestone soil, *Warnock 10625* (LL, SMU). Brown Co.: Brownwood, open calcareous ground, *E. J. Palmer 29530* (MO). Comanche Co.: Highway 6 at Leon River 6.75 mi SE of DeLeon, highway shoulder, *Cory 58088* (SMU). Hamilton Co.: road margin E side of Hico, gray-brown silt and limestone gravel, *Shinners 15937* (SMU). McLennan Co.: Waco, roadside sand, *L. D. Smith 805* (TEX). Navarro Co.: Frost, *Mitchan 45* (TEX). El Paso Co.: El Paso, *Tharp 3541* (TEX, US). Hudspeth Co.: between Nulo and Harris Siding, *Ferris & Duncan 2449* in part (CAS, MO, NY). Culberson Co.: near creekside 6 mi NE of Pine Springs, limestone hills, *Waterfall 5768* (GH, MO). Reeves Co.: roadside 14 mi SSE of Orla, fine sandy silt, *Shinners 31060* (GH, SMU). Ward Co.: 2 mi W of Pyote Air Base, gypsum flats, *Waterfall 5492* (CAS, GH, MO, NY). Crane Co.: 13 mi N of Imperial, 2850 ft, *Warnock 15464* (LL). Tom Greene Co.: roadside 7 mi NE of San Angelo, sandy silt, *Shinners 26337* (SMU). McCulloch Co.: 5.5. mi NW of Fife, *Cory 43444* (GH). Bell Co.: Leon River bottom 2.1 mi NE of old Tennessee Valley Church site, *York & York 54565* (SMU, TEX). Pecos Co.: near Pecos River 3 mi from Sheffield, cultivated field, *Ferris & Duncan 2973* (CAS, DS, MO, NY). Schleicher Co.: Colcote Ranch, 11.5 mi N of Eldorado, *Cory 32555* (GH). Williamson Co.: road junction 0.5 mi N of Round Rock, open grassy field, *Gould 8412* (ARIZ, SMU, UC). Brazos Co.: College Station, *Reeves 709* (LL, SMU). Jeff Davis Co.: Geo. Jones Ranch, Davis Mts., flat, *Hinckley 1194* (ARIZ, F, NY, TEX). Presidio Co.: ca. 4–5 mi E of old Rawls ranch, 50 mi S of Marfa, alluvial soil near large dry creek, *Hinckley 2615* (GH, LL). Brewster Co.: Chisos Mts., *Muller 8058* (F, GH, MICH, MO, NY, TEX, US). Terrell Co.: Blackstone Ranch, 13 mi S of Sheffield, cedar-sotol mesa-top, 2750 ft, *Webster 400* (TEX). Crockett Co.: 15 mi N of Juno, limestone soil, 1500 ft, *Warnock & McBryde 15178* (LL, TEX). Sutton Co.: Roy Hudspeth, *Cory 1847* (GH). Blanco Co.: near Blowout Cave, dry sandy soil, *Johnson 290* (TEX). Travis Co.: near Waller Creek, dry calcareous soil, *Harpin, Waldorf & Barkley 13072* (CAS, MO, NY, PH, POM, TEX, UC). Val Verde Co.: Shumla, *Tharp,* 10 Oct 1936 (GH, MO, SMU, UC). Edwards Co.: Highway 55 NW of Rocksprings, *Hardy 43485* (GH). Kerr Co.: Kerrville, *Heller 1777* (ARIZ, BM, F, GH, MICH, MO, MSC, NY, PH, POM, UC, US). Hays Co.: San Marcos, *Fisher 96* (US). Caldwell Co.: Lockhart, *Mackensen 92* (F). Harris Co.: Houston, *Thurow 4* (F, UC, US). Uvalde Co.: Uvalde, *E. J. Palmer 11025* (DS, MO, US). Bexar Co.: San Antonio, clayey soil, *Lindheimer 342* (BM GH, MO, NY, PH, SMU, US). DeWitt Co.: without locality, *Reidel,* 27 Aug 1941 (TEX). Maverick Co.: Farm Road 1021 8 mi S of Eagle Pass, fine sandy silt, *de Anda, Salazar & McCart 8366* (ARIZ, LL, SMU, TEX). Atascosa Co.: dry roadside ditch 1 mi SSE of Pleasanton, black silty clay, *Shinners 24099* (SMU). Karnes Co.: Karnes City Cemetery, dry silty loam, *Johnson 1055* (SMU, TEX). Goliad Co.: Goliad, sandy prairies. *Williams 36* (PH). LaSalle Co.: State Highway 97, 2 mi W of Los Angeles, gray calcareous marl, *Gongora, Garza & McCart 8508* (SMU, TEX). McMullan Co.: 8 mi E of Tilden, gray silty clay and limestone gravel, *Shinners 16971* (SMU). Webb Co.: Laredo, *Palmer 131* in part (F, MICH, NY, US). Kleberg Co.: Kingsville, dry neglected soil, disturbed areas, *Bogusch 11845* (US). Zapata Co.: State Highway 496, 5 mi NE of Bustamante, sandy loam,

Garcia, Esquivel & McCart 55 (SMU). MISSISSIPPI. Oktibbeha Co.: Mississippi Agricultural College, *Pollard 1295* (GH, MO, NY, US).

MEXICO. SONORA: Río Bavispe, near Colonia Oaxaca, *S. S. White 666* in part (MICH). CHIHUAHUA: Carretas, 4800 ft, *S. S. White 2527* (GH, MEXU, MICH); Meoqui, *LeSueur 741* (F, MO, SMU, TEX, UC). COAHUILA: Monclova, *Palmer 131A* (GH, MICH, NY, PH); Saltillo, *Palmer 295* (BM, F, GH, MO, NY, UC, US). NUEVO LEON: Linares, *Frye & Frye 2532* (DS, GH, MO, NY, RSA, UC, US); Monterrey, 1800 ft, *Fisher 41* in part (CAS, DS, F). DURANGO: Durango and vicinity, *Palmer 477* (BM, F, GH, MEXU, MO, NY, UC, US). ZACATECAS: Hacienda de Cedros, flats, *Lloyd 178* (US). SAN LUIS POTOSI: Charcas, *Whiting 1024* (MICH). AGUASCALIENTES: Aguascalientes, *Hartweg 24* (BM). GUANAJUATO: roadside ditch 14 mi NW of Salamanca, sand, *Waterfall & Wallis 13898* (F, SMU). QUERETARO: near Querétaro, *Fr. Basile 118, 162* (US). HIDALGO: Zimapán, *Coulter 780* in part (GH). MEXICO: Penot de los Baños, *Berlandier 617* (BM).

PERU. HUANUCO: along trail near Huánuco, ca. 7000 ft, *Macbride & Featherstone 2335* (F). LIMA: near Lima-Oroya highway at km 70 E of Lima, heavy rocky soil, 1800 m, *Goodspeed &Weberbauer 33067* (GH, MO, UC, US). HUANCAVELICA: Río Mantaro valley below Pampas, 1300–1400 m, *Weberbauer 6516* in part (F, GH). ICA: between Cocharcas and Quilque, sandy soil, *Ferreyra 580* in part (US). CUZCO: Chuyani, right bank of Río Apurímac, sandy and rocky slopes, 2850 m, *Vargas C. 9725* (F, GH, MO, UC). APURIMAC: Río Pachachaca 20 km N of Abancay, sandy soil, 2000 m, *Stork, Horton & Vargas C. 10527* (UC).

COMMON NAMES. It is surprising that such a widespread plant has so few common names. Those that have been reported are Carpet Weed (Texas); Contrayerba (Arizona); Golondrina (Chihuahua); Guesillos (Texas); Jepo (Peru); and Ray Weed (Texas).

TAXONOMY. The name *Kalstroemia laetevirens* has been applied to somewhat larger than average and upright specimens from Arizona and New Mexico, but these individuals simply represent one extreme in the variation to be found in *K. parviflora*.

VARIATION. In addition to the variation in size alluded to above, there may be a considerable amount of variation in the species in terms of leaflet number (three to six pairs), sepal length in fruit (from extending only to the tops of the mature mericarps to the base of the stigma), beak length (from as long as to three times the length of the fruit body), and beak pubescence (trichomes appressed to spreading or absent). However, these characters appear to vary independently and show no ecological or geographical correlation and cannot be used in defining subspecific taxa in this somewhat variable species.

Specimens of *Kallstroemia parviflora* from Peru show a certain amount of variation in flower size and sepal and style length, but

this variation is not nearly so wide as that found for the species in North America.

RELATIONSHIPS. The close relationship of *Kallstroemia parviflora* and *K. grandiflora* was first indicated by Norton. The differences between these two species are discussed above.

17. **Kallstroemia hintonii** D. M. Porter, *sp. nov.*

TYPE: Mexico, Michoacán: Apatzingán District, Tepalcatepec, elev. 400 m, woods, fl. light yellow, 25 Aug. 1938, *Geo. B. Hinton 12106* (ARIZ, holotype; CAS, LL, NY, PH, TEX, US, isotypes). This species is named for George Boole Hinton, Sr. (1883–1943), mining engineer and well-known collector of the flora of Mexico.

Annua (raro perennis?); caules prostrati, ad 4 dm longi vel longiores, hirsuti, trichomata lutea, et sericea, trichomata alba, antrorsa; stipulae 5–11 mm longae, 1–2 mm latae; folia elliptica, 2.5–8.5 cm longa, 1.5–4 cm lata, pares foliolorum 5–7, foliola elliptica vel ovata, appresse hirsuta, 9–19 mm longa, 3–8 mm lata, pares in medio laminae maxima; pedunculi quam folia subtendentia multo longiores, flores ergo folia excedentes, ad apicem vix incrassati, anthesin 3–10.5 cm longi, in fructu 5–10.5 cm longi, recti et patentes; flores pentameri in diametro 3–6 cm; sepala lanceolata, 8–12 mm longa, 1.5–3 mm lata, persistentia, quam petala 1/2 breviora, hirsuta, trichomata lutea, anthesin stylum excedentia, in fructu mericarpia amplectentia, quam basin stigmatis longa, margines scariosi, deinde involuti, persistentia; petala alba, deinde luteola, in siccis aurantiaca, ad basin luteo-viridia vel raro rubra, obovata, truncata, ad apicem irregulariter erosa, 15–30 mm longa, 9–20 mm lata, marcescentia; stamina et stylus aequilongus; filamenta ad basin alata; antherae ovoideae, in diametro 1.5–2 mm, rubro-aurantiacae sicut pollen; ovarium ovoideum, glabrum, 1–2 mm in diametro; stylus 6–9 mm longus, cylindricus, ad basin conicus, glaber; stigma clavatum, 10–porcatum, ca. 1 mm longum, papillosum; fructus late ovoideus, 4–5 mm altus, 6–8 mm latus, glaber; rostrum 8–11 mm longum, quam fructificatio duplo longius, cylindricum, ad basin conicum, glabrum; mericarpia 5 mm alta, 2 mm lata, abaxialiter rugosa, latera foveolata, adaxialiter subangulata.

Annual (occasionally perennial?); *stems* prostrate, to 4 dm long or longer, hirsute with yellow and sericeous with white apically-directed trichomes; *stipules* 5–11 mm long, 1–2 mm wide; *leaves* elliptical, 2.5–8.5 cm long, 1.5–4 cm wide; *leaflets* 5–7 pairs, elliptical to ovate, appressed-hirsute, 9–19 mm long, 3–8 mm wide, middle pairs largest; *peduncles* much longer than subtending leaves, extending flowers well above herbage, scarcely thickened distally, 3–10.5 cm long in flower, 5–10.5 cm long in fruit and straight and spreading; *flowers* pentamerous, 3–6 cm in diameter; *sepals* lanceolate, 8–12 mm long, 1.5–3 mm wide, ca. 1/2 as long as petals, hirsute with yellow trichomes, longer than style in flower, in fruit clasping but not entirely covering mature mericarps and reaching to stigma base, only scarious margins becoming involute, persistent; *petals* white, yellowing with age and drying orange, base yellow-green or rarely red, obovate, truncate, apex irregularly notched, 15–30 mm long, 9–20 mm wide, marcescent; *stamens* as long as style; *filaments* winged at base; *anthers* ovoid, 1.5–2 mm in diameter, they and pollen red-orange; *ovary* ovoid, glabrous, 1–2 mm in diameter; *style* 6–9 mm long, cylindrical, base conical, glabrous; *stigma* clavate, 10–ridged,

ca. 1 mm long; *fruit* broadly ovoid, 4–5 mm high, 6–8 mm wide, glabrous; *beak* 8–11 mm long, ca. twice length of fruit body, cylindrical, base conical, glabrous; *mericarps* 5 mm high, 2 mm wide, abaxially cross-ridged and slightly keeled, sides pitted, adaxial edge slightly angled. *Fig. 17a, 17b. Map 11.*

FLOWERING DATES. Known to flower in August, September, and December.

DISTRIBUTION AND HABITAT. Found along roadsides at elevations from 300 to 400 m in the general vicinity of Apatzingán, Michoacán, Mexico *(Map 11). Kallstroemia maxima* and *K. pubescens* are known to occur in the same area.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia hintonii* is easily recognized by its combination of prostrate stems, elliptical leaves, five to seven pairs of appressed-hirsute leaflets, fruiting peduncles 5–10½ cm long, extending the flowers well above the herbage, white flowers (petal bases yellow-green or red) 3–6 cm in diameter, hirsute sepals clasping the mature mericarps but not entirely covering them and reaching to the stigma base, the filaments winged at the base, red-orange anthers and pollen, cylindrical style three or four times as long as the ovary, clavate ten-ridged stigma, broadly ovoid glabrous fruit 4–5 mm high and 6–8 mm wide, beak about twice as long as the fruit body, and abaxially cross-ridged and slightly keeled mericarps about 2 mm wide. *Kallstroemia hintonii* is unlikely to be confused with any other species of the genus.

SPECIMENS EXAMINED. MEXICO. MICHOACAN: roadside near Apatzingán, 1000 ft, *Barr, Dennis & Hevly 62–654* (ARIZ); 1 mi S of Apatzingán, *Leavenworth 497* (MICH, MO); roadside 6 mi W of Apatzingán toward Aguililla, *Porter 1426* (DS, GC, GH, IJ, MEXU); cultivated valley 11 mi E of Cuatro Caminos toward La Huacana, edge of raised road, 310 m, *Porter 1414* (GH); dusty roadside 13 mi E of Cuatro Caminos, rocky valley alluvium, 310 m, *Porter 1413A* (GH).

VARIATION. Petal color in *Kallstroemia hintonii* varies from white aging to yellow to white with a red basal spot.

The collections *Porter 1413A* and *Porter 1414* are rather depauperate, but in all morphological respects they appear to be properly placed in this taxon.

RELATIONSHIPS. *Kallstroemia hintonii* shows no close morphological relationship to any other species in the genus.

Excluded Species

Kallstroemia angustifolia (R. Br. in Sturt) Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3(4):88. 1890. = *Tribulopis angustifolia* R. Br. in Sturt, Appendix 70. 1849.

Kallstroemia bicolor (F. Muell.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulopis bicolor* F. Muell., Frag. Phyt. Austral. 1:47. 1858.

Kallstroemia cistoides (L.) Endl., Ann. Naturg. Mus. Wein 1:184. 1836. = *Tribulus cistoides* L., Sp. Pl. 1:387. 1753.

Kallstroemia hirsuta (Benth.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus hirsutus* Benth., Fl. Austral. 1:289. 1863.

Kallstroemia hystrix (R. Br. in Sturt) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus hystrix* R. Br. in Sturt, *op. cit.* 69. 1849.

Kallstroemia macrocarpa (F. Muell. in Benth.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus macrocarpus* F. Muell. in Benth., *loc. cit.*

Kallstroemia minuta (Leichh. ex Benth.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus minutus* Leichh. ex Benth., *op. cit.* 291. 1863.

Kallstroemia pentandra (R. Br. in Sturt) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulopis pentandra* R. Br. in Sturt, *op. cit.* 70. 1849.

Kallstroemia platyptera (Benth.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus platypterus* Benth., *op. cit.* 289. 1863.

Kallstroemia ranunculiflora (F. Muell.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus ranunculiflorus* F. Muell., *op. cit.* 48. 1858.

Kallstroemia solandri (R. Br. in Sturt) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulopis solandri* R. Br. in Sturt, *op. cit.* 70. 1849.

Literature Cited

Agababian, V. Sh. 1964. The morphological types of pollen and taxonomy of the family Zygophyllaceae. [In Russian] Izv. Akad. Nauk Armian. SSR. Biol. 17(12):39–45.

Andersson, N. J. 1861. Über die Vegetation der Galapagos-inseln. Linnaea 31:571–631.

Andres, L. A., & G. W. Angalet. 1963. Notes on the ecology and host specificity of *Microlarinus lareynii* and *M. lypriformis* (Coleoptera: Curculionidae) and the biological control of puncture vine, *Tribulus terrestris*. Journ. Econ. Entomol. 56:333–340.

Anonymous. 1963. Arizona-Poppy *(Kallstroemia grandiflora)*. Saguaroland Bull. 17:72.

Arnoldo, Fr. M. 1964. Zakflora. Wat in het wild groeit em bloeit op Curaçao Aruba en Bonaire. Martinus Nijhoff, The Hague.

Axelrod, D. I. 1950. Contributions to paleobotany. VI. Evolution of desert vegetation in western North America. Carnegie Inst. Wash. Publ. 590:215–306.

————————. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 26:433–509.

Baillon, H. 1872. Observations sur les rutacées. Adansonia 10:299–333.

————————. 1875. The Natural History of Plants. Vol. 4. M. M. Hartog, trans. L. Reeve, London.

Baker, E. G. 1898. New Somaliland polypetalae. Journ. Bot. 36:2–6.

Baker, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9:347–349.

Bennet, S. S. R. 1965. Genus *Kallstroemia* Scop. (Zygophyllaceae)—new to Indian flora. Indian Forest. 91:281–283.

BENTHAM, G., & J. D. HOOKER. 1862. Genera Plantarum. Vol. 1. L. Reeve, London.
————————, & ————————. 1867. Addenda et Corrigenda. pp. 953–1009 in Genera Plantarum. Vol. 1.
BERRY, E. W. 1928. Tertiary fossil plants from the Argentine Republic. Proc. U. S. Nat. Mus. **73**(27):1–27.
————————. 1932. Fossil plants from Chubut Territory collected by the Scarritt Patagonian Expedition. Amer. Mus. Novitiates **563**:1–10.
BOLDINGH, I. 1914. Flora of the Dutch West Indian Islands. Vol. 2. The Flora of Curaçao, Aruba, and Bonaire. E. J. Brill, Leiden.
BONET, F., & J. RZEDOWSKI. 1962. La vegetación de las islas del Arrecife Alacranes, Yucatán (Mexico). An. Esc. Nac. Cienc. Biol. Mex. **11**:15–60.
BREWER, W. H., & S. WATSON. 1876. Zygophyllaceae. pp. 91–92 in W. H. Brewer, S. Watson, & A. Gray, Botany of California. Vol. 1. Welch, Bigelow, & Co., Cambridge, Massachusetts.
BRITTON, N. L., & A. BROWN. 1913. An Illustrated Flora of the Northern United States, Canada, and the British Possessions. Ed. 2. Vol. 2. Charles Scribner's Sons, New York.
BROWN, R. 1849. Botanical appendix. pp. 66–92 in C. Sturt, Narrative of an Expedition into Central Australia, during the years 1844, 1845, and 1846. Vol. 2. London.
BROWN, W. H. 1938. The bearing of nectaries on the phylogeny of flowering plants. Proc. Amer. Philos. Soc. **79**:549–595.
BROWNE, P. 1756. The Civil and Natural History of Jamaica. London.
CABRERA, A. L. 1951. Territorios fitogeográficos de la República Argentina. Bol. Soc. Argent. Bot. **4**:21–65.
CANNON, W. A. 1911. The root habits of desert plants. Carnegie Inst. Wash. Publ. 131.
CÁRDENAS, M. 1945. Aspecto general de la vegetación de Bolivia. pp. 312–313 in F. Verdoorn, ed., Plants and Plant Science in Latin America. Ronald Press, New York.
CARLETON, M. A. 1892. Observations on the native plants of Oklahoma Territory and adjacent districts. Contr. U. S. Nat. Herb. **1**:220–232.
CHIOVENDA, E. 1916. Le Colezioni Botaniche della Missione Stefanini-Paoli nella Somalia Italia. Galletti e Cocci, Firenze.
————————. 1917. Plantae novae vel minus notae e regione Aethiopicae. Bull. Soc. Bot. Ital. **1917**:21–27.
————————. 1929. Flora Somala. Vol. 1. Sindacteto Italiano Arti Grafiche, Rome.
CLEMENTS, F. E. 1920. Plant indicators. The relation of plant communities to process and practice. Carnegie Inst. Wash. Publ. 290.
COCKERELL, T. D. A. 1896. The bees of the genus *Perdita* F. Smith. Proc. Acad. Nat. Sci. Phila. **1896**:25–107.
DESCOLE, H. R., C. A. O'DONELL, & A. LOURTEIG. 1939. Zigofiláceas nuevas. Lilloa **4**:217–227.
————————, ————————, & ————————. 1940. Revisión de las zigofiláceas argentinas. *op. cit.* **5**:257–343.
DON, G. 1831. A General System of Gardening and Botany. Vol. 1. London.
DUPREE, A. H. 1959. Asa Gray. Belknap Press of Harvard Univ. Press, Cambridge, Mass.
EMORY, W. H. 1848. Notes of a military reconnaissance, from Fort Leavenworth, in Missouri, to San Diego, in California, including part of the Arkansas, Del Norte, and Gila Rivers. U. S. Senate, 30th Congr., 1st Sess. Exec. Doc. No. 7. Washington, D. C.

ENGLER, A. 1890. Zygophyllaceae. pp. 74–93 in A. Engler & K. Prantl, eds., Die natürlichen Pflanzenfamilien. Band 3, Tiel 4. Verlag von Wilhelm Engelmann, Leipzig.
————————. 1915. Die Pflanzenwelt Afrikas. Die Vegetation der Erde. Band IX. Verlag von Wilhelm Engelmann, Leipzig.
————————. 1931. Zygophyllaceae. pp. 144–181 in A. Engler & K. Prantl, eds., Die natürlichen Pflanzenfamilien, Auf. 2. Band 19a. Verlag von Wilhelm Engelmann, Leipzig.
ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. Angiosperms. Chronica Botanica, Waltham, Mass.
ERNST, A. 1876. Botanische Miscellaneen. I. Zwei Fälle von ausserordentlichen Vitalität der Samen. Bot. Zeit. 34:33–35.
EVENARI, M. 1949. Germination inhibitors. Bot. Rev. **15**:153–194.
FAWCETT, W., & A. B. RENDLE. 1920. Flora of Jamaica. Vol. 4. Dicotyledons. Families Leguminosae to Callitrichaceae. British Museum (Natural History), London.
FOSTER, R. C. 1958. A catalogue of the ferns and flowering plants of Bolivia. Contr. Gray Herb. **184**:1–223.
FRANZE, B. 1927. Die Niederschlagsverhältnisse in Südamerika. Petermanns Mitt., Erg. Hft. Nr. 193.
FRYXELL, P. A. 1957. Mode of reproduction of higher plants. Bot. Rev. **23**:135–233.
GOLDSMITH, G. W., & A. L. HAFENRICHTER. 1932. Anthokinetics. The physiology and ecology of floral movements. Carnegie Inst. Wash. Publ. 420.
GÓMEZ DE LA MAZA, M. 1889. Ensayo de Farmacofigologia Cubana. La Propaganda Literaria, Havana.
GRAY, A. 1852. Plantae Wrightianae Texanae Neo-Mexicanae. Part 1. Smithsonian Inst., Washington, D. C.
————————. 1853. Plantae Wrightianae Texanae Neo-Mexicanae. Part 2. Smithsonian Inst., Washington, D. C.
————————. 1887. Contributions to American Botany. I. Revision of some polypetalous genera and orders precursory to the Flora of North America. Proc. Amer. Acad. **22**:270–306.
————————. 1897. Zygophyllaceae. [Notes by B. L. Robinson.] pp. 352–356 in A. Gray & S. Watson, Synoptical Flora of North America. Vol. 1, Pt. 1. B. L. Robinson, ed. American Book Co., New York.
GUPPY, H. B. 1906. Observations of a Naturalist in the Pacific between 1896 and 1899. Vol. 2. Plant Dispersal. Macmillan, London.
HOLZINGER, J. M. 1892. List of plants collected by C. S. Sheldon and M. A. Carlton in Indian Territory in 1891. Contr. U. S. Nat. Herb. 1:189–219.
IRVINE, F. R. 1930. Plants of the Gold Coast. Oxford Univ. Press, London.
JACKSON, B. D. 1893. Biographical notes. II "Botany of Beechey's Voyage" and "Flora of North America." Journ. Bot. 31:297–299.
JEPSON, W. L. 1936. Flora of California. Vol. 2. Associated Students Store, Univ. of California, Berkeley.
JOHNSON, E. 1936. Puncture vine. pp. 68–70 in W. S. Ball, A. S. Crafts, B. A. Madson & W. W. Robbins, Weed Control. Calif. Agr. Ext. Serv. Circ. 97.
KEARNEY, T. H., & R. H. PEEBLES. 1939. Arizona plants: New species, varieties, and combinations. Journ. Wash. Acad. Sci. **29**:474–492.
KEAY, R. W. J. 1955. Revision of the "Flora of West Tropical Africa." VII. Kew Bull. **10**:137–141.
KINGSBURY, J. M. 1964. Poisonous Plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, N. J.

KOLLER, D. 1955. Germination regulating mechanisms in some desert seeds. II. *Zygophyllum dumosum* Boiss. Palestine Journ. Bot., Ser. J. 6:151–157.
LANJOUW, J., & F. A. STAFLEU. 1964. Index Herbariorum. Part 1. The Herbaria of the World. Ed. 5. Regnum Vegetabile, Vol. 31. Utrecht.
LEAVENWORTH, W. C. 1940. (Data on label of herbarium specimen of *Kallstroemia hintonii* at MICH and MO; *Leavenworth 497*).
LEOPOLD, A. S. 1950. Vegetation zones of Mexico. Ecology 31:507–518.
LEWIS, H. 1963. The taxonomic problem of inbreeders, or how to solve any taxonomic problem. Regnum Vegetabile **27**:37–44.
VON LUETZELBURG, P. 1923. Estudio Botanico de Nordéste. Vol. 3 Ministerio de Viação e Obras Publicas, Rio de Janeiro.
MACBRIDE, J. F. 1930. Spermatophytes, mostly Peruvian. II. 4. Other Peruvian plants, chiefly new species. Field Mus. Nat. Hist., Bot. Ser. **8**:113–129.
————————. 1949. Flora of Peru. Part 3, No. 2. *op. cit.* **13**:511–777.
MACFADYEN, J. 1837. The Flora of Jamaica. Longman, Orme, Brown. Green, & Longmans, London.
MARSHALL, H. S. 1950. The Botany of Beechey's Voyage. Kew Bull. **1950**:33.
MARTIN, P. S. 1963. The Last 10,000 Years. A Fossil Pollen Record of the American Southwest. Univ. of Arizona Press, Tucson.
MAURITZON, J. 1934. Etwas über die Embryologie der Zygophyllaccen sowie einige Fragmente über die der Humiriaceen. Bot. Not. **87**:409–422.
MCGINNIES, W. G. 1922. (Data on label of herbarium specimen of *Kallstroemia grandiflora* at ARIZ; *McGinnies 25*).
MCVAUGH, R. 1956. Edward Palmer, Plant Explorer of the American West. Univ. of Oklahoma Press, Norman.
MILLSPAUGH, C. F. 1900. Plantae Utowanae. Plants collected in Bermuda, Porto Rico, St. Thomas, Culebras, Santo Domingo, Jamaica, Cuba, The Caymans, Cozumel, Yucatan, and the Alacran Shoals. Dec. 1898 to Mar. 1899. I. Catalogue of the species. Field Columb. Mus., Bot. Ser. **2**:1–110.
————————. 1916. Vegetation of Alacran Reef. Field Mus. Nat. Hist., Bot. Ser. **2**:401–431.
MUNZ, P. A. 1959. A California Flora. Univ. of California Press. Berkeley.
————————. 1962. California Desert Wildflowers. Univ. of California Press, Berkeley.
NORTON, J. B. S. 1898. Notes on some plants, chiefly from the southern United States. Ann. Rpt. Mo. Bot. Gard. **9**:151–157.
PENROSE, B. 1952. Travel and Discovery in the Renaissance, 1420–1620. Harvard Univ. Press, Cambridge, Mass.
PEREZ ARBELÁEZ, E. 1956. Plantas Útiles de Colombia. Librería Colombiana, Bogotá.
PITTIER, H. 1957. Ensayo sobre Plantas Usuales de Costa Rica. Ed. 2. Publ. Univ. Costa Rica, Ser. Cienc. Nat. No. 2.
PORTER, D. M. 1963. The taxonomy and distribution of the Zygophyllaceae of Baja California, Mexico. Contr. Gray Herb. **192**:99–135.
RAVEN, P. H. 1963. Amphitropical relationships in the floras of North and South America. Quart. Rev. Biol. **38**:151–177.
RICHARD, A. 1845. Historie Physique, Politique et Naturelle de l'Ile de Cuba. Botanique–Plantes Vasculares. Arthus Bertrand, Paris.
ROBINSON, B. L. 1902. Flora of the Galápagos Islands. Proc Amer. Acad. **38**:75–270.
ROGERS, A. D. 1942. John Torrey: A Story of North American Botany. Princeton Univ. Press, Princeton, N. J.

ROLLINS, R. C. 1952. Taxonomy today and tomorrow. Rhodora **54**:1–19.
————————. 1957. Taxonomy of the higher plants. Amer. Journ. Bot. **44**:188–196.
ROSE, J. N. 1891. List of plants collected by Dr. Edward Palmer in western Mexico and Arizona in 1890. Contr. U. S. Nat. Herb. **1**:91–116.
————————. 1892. List of plants collected by the USS Albatross in 1887–'91 along the western coast of America. 2. List of plants from the Galápagos Islands. **1**:136–138.
RUÍZ LEAL, A. 1947. Dos zigofiláceas nuevas para la flora cuyana. Haumania **1**:11–14.
————————. 1951. *Kallstroemia tucumanensis* Desc., O'Don. et Lourt. (Zygophyllaceae) en las immediaciones del Cerro de la Gloria. Rev. Fac. Cienc. Agr. **3**:27–29.
RUNYON, E. H. 1930. Germination and establishment of *Covillea*. Carnegie Inst. Wash. Yearbook **29**:225–226.
SALISBURY, E. J. 1942. The Reproductive Capacity of Plants. G. Bell & Sons, London.
————————. 1961. Weeds and Aliens. Collins, London.
SCHINZ, H. 1895. Beitrage zur Kenntnis der Afrikanischen Flora. III. Bull. Herb. Boiss. **3**:373–441.
SCHOLZ, H. 1964. Zygophyllaceae. pp. 251–252 in H. Melchior, ed., A. Engler's Syllabus der Pflanzenfamilien. Ed. 12. Vol. 2. Gebrüder Borntraeger, Berlin.
SCHWEICKERDT, H. G. 1937. An account of the South African species of *Tribulus* Tourn. ex Linn. Bothalia **3**:159–178.
SHELFORD, V. E. 1963. The Ecology of North America. Univ. of Illinois Press, Urbana.
SHREVE, F. 1937. The vegetation of the Cape Region of Baja California. Madroño **4**:105–113.
————————. 1942. The desert vegetation of North America. Bot. Rev. **8**:195–246.
————————. 1951. Vegetation of the Sonoran Desert. Carnegie Inst. Wash. Publ. 591.
SIMPSON, G. G. 1965. Mammalian evolution on the southern continents. pp. 211–234 in Simpson, The Geography of Evolution. Chilton, Philadelphia.
SLOANE, H. 1696. Catalogus Plantarum quae in Jamaica sponte proveniunt. London.
————————. 1707. A Voyage to the Islands Madera, Barbados, Nieves, S. Cristophers and Jamaica, with the Natural History of the Herbs and Trees, Four-footed Beasts, Fishes, Birds, Insects, Reptiles, etc. of the Last of those Islands, etc. Vol. 1. London.
SMITH, A. C., & I. M. JOHNSTON. 1945. A phytogeographic sketch of Latin America. pp. 11–18 in F. Verdoorn, ed., Plants and Plant Sciences in Latin America. Chronica Botanica, Waltham, Mass.
STANDLEY, P. C. 1928. Flora of the Panama Canal Zone. Contr. U. S. Nat. Herb. Vol. 27.
————————. 1940. (Data on label of herbarium specimen of *Kallstroemia pubescens* at GH: *Standley* 73599).
————————, & J. A. STEYERMARK. 1946. Flora of Guatemala. Fieldiana: Bot. Vol. 24, Pt. 5.
STEARN, W. T. 1957. Introduction. pp. 1–116 in C. Linnaeus, Species Plantarum. Vol. 1. Facsimile of the First Edition. The Ray Society, London.
STEBBINS, G. L., JR. 1947. Evidence on rates of evolution from the distribution of existing and fossil plant species. Ecol. Mon. **17**:149–158.

———————. 1949. Rates of evolution in plants. pp. 229–242 in G. L. Jepson, G. G. Simpson & E. Mayr, eds., Genetics, Paleontology, and Evolution. Princeton Univ. Press, Princeton, N. J.
———————. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York.
———————. 1952. Aridity as a stimulus to plant evolution. Amer. Nat. **86**:33–44.
———————. 1957. Self fertilization and population variability in the higher plants. *op. cit.* **91**:337-354.
Svenson, H. K. 1946a. Vegetation of the coast of Ecuador and Peru and its relation to that of the Galápagos Islands. I. Geographical relations of the flora. Amer. Journ. Bot. **33**:394–426.
———————. 1946b. Vegetation of the coast of Ecuador and Peru and its relation to that of the Galápagos Islands. II. Catalogue of plants. *op. cit.* **33**:427–498.
Timberlake, P. H. 1954. A revisional study of the bees of the genus *Perdita* F. Smith, with special reference to the fauna of the Pacific Coast (Hymenoptera, Apoidea). I. Univ. Calif. Publ. Entomol. **9**:345–432.
———————. 1960. A revisional study of the bees of the genus *Perdita* F. Smith, with special reference to the fauna of the Pacific Coast (Hymenoptera, Apoidea). IV. *op. cit.* **17**:1–156.
Torrey, J. 1859. Botany of the boundary. pp. 29–270 in W. H. Emory, Report on the United States and Mexican Boundary Survey. U. S. House of Representatives, 34th Contr., 1st. Sess. Exec. Doc. No. 135. Washington, D. C.
———————, & A. Gray. 1838. A Flora of North America. Vol. 1 Wiley & Putnam, New York.
Tosi, J. A., Jr. 1960. Zonas de vida natural en el Perú. Inst. Interamer. Cienc. Agr. Bot. Tec. No. 5, San José, Costa Rica.
Vail, A. M., & P. A. Rydberg. 1910. Zygophyllaceae, No. Amer. Fl. **25**:103–116.
Waterfall, U. T. 1946. Observation on the desert gypsum flora of Southwest Texas and adjacent New Mexico. Amer. Midl. Nat. **36**:456–466.
Watson, S. 1876. Botanical contributions. III. Descriptions of new species of plants, chiefly Californian, with revisions of certain genera. Proc. Amer. Acad. **11**:121–148.
———————. 1889. Upon a collection of plants made by Dr. E. Palmer, in 1887, about Guaymas, Mexico, at Muleje and Los Angeles Bay in Lower California, and on the Island of San Pedro Martir in the Gulf of California. *op. cit.* **24**:36–82.
Westeroüen van Meetenen, 1883. Surinaamsche Planten en Cultuurgewassen, Boomen en Houtsoorten. Amsterdam.
Wight, R., & G. A. W. Arnott. 1834. Prodromus Florae Peninsulae Indiae Orientalis. Vol. 1. Parbury, Allen, London.
Williams, L. 1935. A new *Kallstroemia* from Texas. Ann. Mo. Bot. Gard. **22**:49–50.
Wright, S. 1940. Breeding structure of populations in relation to speciation. Amer. Nat. **74**:232–248.
Yunker, T. G. 1965. Cuscuta. N. Amer. Fl. Ser. 2, Pt. 4.

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THE SYSTEMATICS AND EVOLUTION OF PEREZIA SECT. PEREZIA (COMPOSITAE)

BERYL SIMPSON VUILLEUMIER[1]

INTRODUCTION

Although the principle of geographic speciation is now considered an axiom of modern evolutionary theory, few studies have been made which actually point out the geographical factors that have influenced it. The investigations which have been made dealt, for the most part, with relatively simple cases of islands and their floras and faunas. During the past six years, Dr. F. Vuilleumier and I have been engaged in a study of the patterns of speciation on a continental area—South America—and, in particular, the flora and fauna of the high Andes. (See Fig. 1 for the major physiographic features of the Andean Cordillera.) Ultimately, we hope to combine evidence from vertebrate animals and diverse groups of Angiosperms.

However, before much progress can be made on such a study, it is essential to have a basic knowledge of the species involved and how they are related. A survey of the literature on Andean plants indicates that it would be impossible to rely on previous publications. Only about 50 genera of high Andean plants have been thoroughly revised within the last 30 years (since the widespread acceptance of the Synthetic Theory of evolution). Most of these did not use modern concepts, and were based on inadequate material.

Therefore, it was found necessary to begin a series of detailed biosystematic revisions of Andean plants to provide the foundation for an analysis of speciation in the Andes, and to determine what barriers have led to reproductive isolation (splitting) of various taxa. This necessity for basic monographic work also created an opportunity to investigate the procedures and methodology of taxonomy itself.

The South American section of *Perezia*, treated here, is widespread in the Andean and Patagonian parts of the continent. Its center of radiation is in the central high Andes, and its origin was probably in temperate montane habitats. Figure 2 gives the distri-

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FIG. 1. The physiography of the Andes. A simplified presentation of the structure and direction of the major mountain chains which make up the Andean Cordillera.

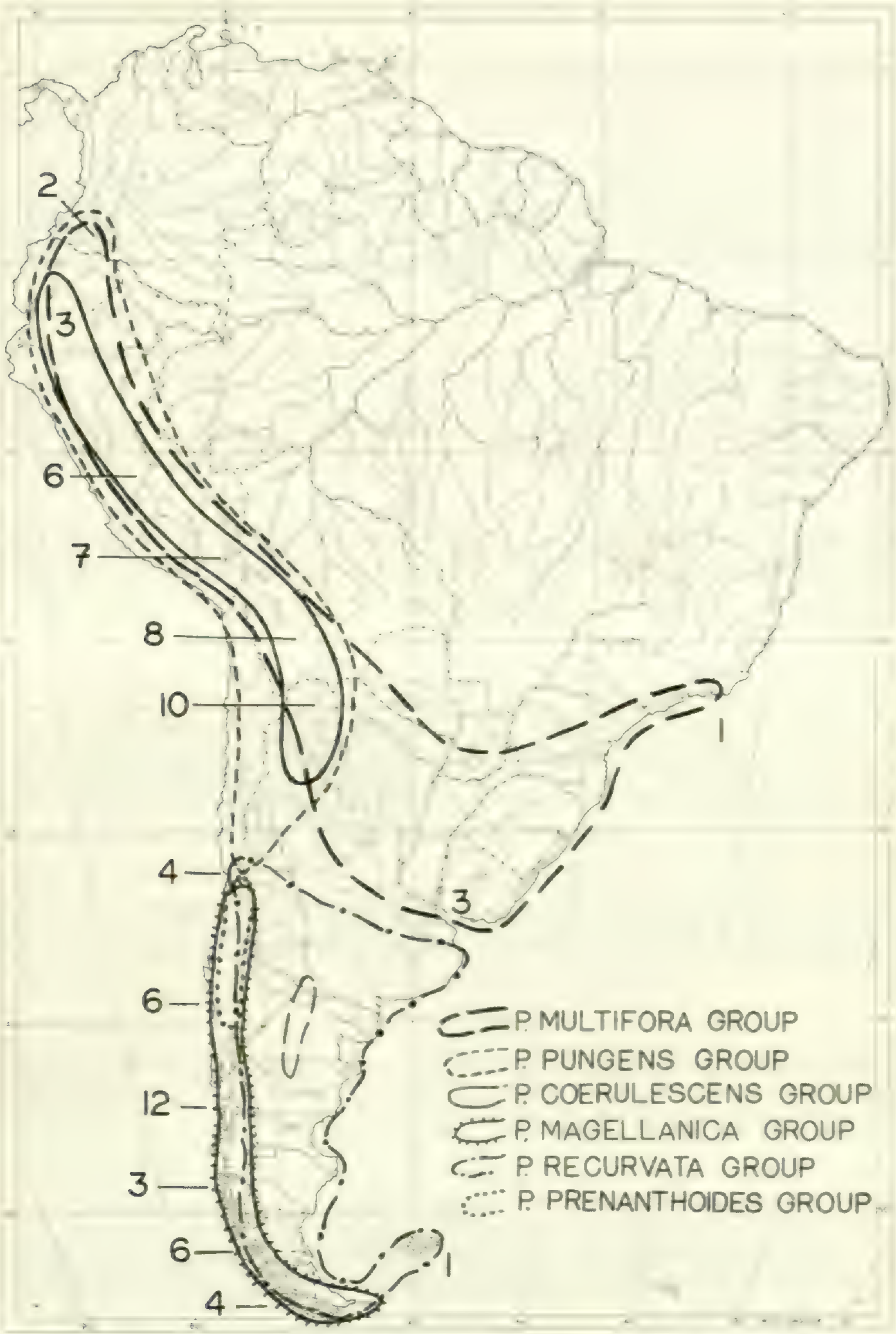


FIG. 2. Distribution of *Perezia* sect. *Perezia* in South America showing the area covered by each of the six species groups (see FIG. 16 for the species in each group). Numbers indicate the total number of species present at various localities.

bution of the six species groups in the section and the number of species found at various places along the Cordillera. Moreover, *Perezia* belongs to a group of genera, the *Nassauviinae* (a subtribe of the *Mutisieae*), which are all linked historically with the Andes. These combined aspects indicated that a detailed revision of *Perezia* sect. *Perezia* would provide a solid initial work on speciation patterns in the Andes, and an opportunity to study the applicability of various taxonomic methods for later work.

To determine which of the modern techniques would be most productive in this taxon and probably also in allied genera, a series of methods, which are currently used in taxonomy were employed. Crossing experiments with high altitude perennials is impossible because of their specialized growth requirements (see Physiological Adaptations). Moreover, the majority of species of *Perezia* sect. *Perezia* are very slow growing and do not form large populations.

The five approaches productively used were: (1) *gross morphology and anatomy;* (2) *palynology;* (3) *cytology;* (4) *chemotaxonomy;* and (5) *numerical taxonomy.* These were pursued as independently and objectively as possible. From each, a partial or fairly complete taxonomy was generated, which could then be compared with, and evaluated in the light of, information provided from other methods. The data were finally integrated and used to produce a synthetic picture, providing a background for the construction of a biologically meaningful classification which would reflect the speciation pattern of the group.

ACKNOWLEDGEMENTS

It is impossible to thank all those who have so generously given me help during the course of this study. I do wish to acknowledge especially the guidance of O. T. Solbrig, R. C. Rollins, C. E. Wood, Jr., B. G. Schubert, and R. A. Howard. D. Moore, R. Hoover, W. E. Niles, and L. Gottlieb all kindly sent seeds of *Perezia*. Both P. H. Raven and L. Sneider provided unpublished chromosome counts and R. Foster wrote the Latin diagnosis. E. Minkoff and W. Bossert were patient enough to teach the methods and principles for the section on numerical taxonomy. I am particularly grateful to F. Vuilleumier whose continuous advice and help made completion of this work possible.

In South America, A. L. Cabrera, M. Ricardi, P. Legname, and O. Tovar all accompanied me on field trips. Gracious hospitality was also extended by numerous other individuals and institutions including: F. Behn; C. Muñoz P., Universidad de Chile; O. Boelcke; A. Willink, A. Digelio, T. Meyer, and P. Legname, Instituto Miguel Lillo; A. Cabrera, Universidad de La Plata; R. Ferreyra, O. Tovar, H-W. and M. Koepcke, Universidad de San Marcos;

I. Kaplan, C. Bonifaz; J. Haffer; W. H. Phelps, Jr.; and A. Benevides and the Cerro de Pasco Corporation of Perú.

During the three years of this study, I was supported by a fellowship from the U. S. Department of Public Health, Education, and Welfare under the NDEA-IV program. Funds for the use of the computer were supplied by NSF Grant GP2723 to the Computer Center of Harvard University. Travel expenses for two field trips were paid by grants from: Bourse fédérale de voyages de la Société helvétique des sciences naturelles (Switzerland); the Fernald Fund of Harvard University; and NSF Grant 3167 to the Evolutionary Biology Committee of the Department of Biology of Harvard University. The maps are used by permission of the Goode Base Maps, University of Chicago, Chicago, Illinois.

Specimens were examined in numerous herbaria in Europe, South America, and the United States and I thank the staffs of these institutions for their hospitality and generosity in lending material. The abbreviations used in the citation of specimens are those listed in Index Herbariorum (Lanjouw and Stafleu, 1964).

Because distribution maps are given here for each species, the specimens cited following each species description are merely representative and do not constitute all the material examined. The type species listed in the synonymy are not relisted in the representative specimens. Except where specifically noted to the contrary, all types cited have been personally examined.

HISTORY OF THE GENUS

In the last part of the eighteenth and early part of the nineteenth century, Europeans were actively exploring the New World for both economic and scientific purposes. Specimens of new plants and animals were constantly being sent back to Europe for identification and description. Sometimes, new genera or families were created for the species which came from the Americas, while in other cases, the new taxa were fitted into European or African genera familiar to Old World naturalists.

In the mid-1770's, Forster, Banks and Solander brought back from Tierra del Fuego a small, delicate, white flowered *Compositae,* which later fell into the hands of Linnaeus' son who placed the species (now *Perezia magellanica*) in *Perdicium* L., a genus of African *Compositae.* In 1790, Vahl described, in the same genus, three other species *(Perezia lactucoides, P. recurvata,* and *P. squarrosa)* collected by Commerson on the voyage of de Bougainville. Humboldt, during his travels a few years later, collected three species of *Compositae* in Ecuador *(P. pungens, P. multiflora,* and *P. pinnatifida)* which he decided in 1809 belonged in *Chaetanthera,* a Ruiz and Pavon genus based on Peruvian collections.

It soon became evident that the number and rate at which new

species, genera, and even families were being described necessitated a thorough examination and revision of the existing taxonomic system to rectify the confusion that had resulted. Alphonse de Candolle was one of the Europeans early to begin a complete reordering of the plant kingdom. Moreover, he was particularly interested in the *Compositae* and published numerous memoirs on the different "families" (tribes) of the group. In 1812, de Candolle published his third memoir, which dealt with a new assemblage of ligulate *Compositae*, the *Labiatiflorae*. He felt that this "belonged between the Cichoraceas and the Cinarocephales" (now included in the *Carduceae*). Although he published the memoir in 1812, he had previously presented the material in a lecture at the University of Geneva in 1808.

Between the time of his original dissertation and the published treatment, de Candolle had found a letter from Marius Lagasca in Spain to the then deceased Bonpland in Paris. It contained the results of a completely independent study he had made on the same group of *Compositae* that de Candolle had placed in his *Labiatiflorae*. Despite the fact that Lagasca called his group an "order," the *Chaenanthophorae*, and used different characters from those employed by de Candolle, the two schemes were very similar. However, the nomenclature of the Spaniard differed from that of his Swiss contemporary.

Because such similar results had been arrived at by both botanists, de Candolle felt that the two studies should be published jointly. He wrote to Lagasca to suggest combining their efforts. Spain was in civil war at the time and Lagasca never received the letter. In 1812, after waiting several years, de Candolle published alone but he paid tribute to Lagasca's work by incorporating into his own account much of the nomenclature used by Lagasca in his letter to Bonpland.

Ironically, Lagasca, isolated in Spain, had published his system in 1811 oblivious to the parallel work being carried on elsewhere. Even more ironically, Lagasca had changed much of the nomenclature from that proposed in his earlier letter to Bonpland. For example, he had indicated that he was going to erect a genus *Clarionea* based on the tiny Fuegian *Perdicium magellanicum*. In his published study, the genus was circumscribed, but the name was changed to *Perezia* in commemoration of Lorenzo Pérez, a former pharmacist from Toledo, Spain. De Candolle, in his

attempt to give credit to Lagasca's work, had used his name, *Clarionea*, for the genus based on *Perdicium magellanicum*. Thus the name *Clarionea* (and several others employed by de Candolle and attributed to Lagasca) became superfluous immediately upon publication. Yet, because of de Candolle's world-wide influence and prestige, and because of the lack of a nomenclatural code, the name *Clarionea* was widely used and persisted until almost the turn of the century.

During the next few decades, many more *Compositae* from South and Central America were described—some obviously closely related to the species initially placed in *Perezia*. Instead of realizing that the new species were congeneric with *Perezia*, European botanists were prone to create new genera for them. For the South American species now considered to belong in *Perezia*, Cassini erected *Drozia*, redefined *Clarionea*, and recognized *Perezia* and *Homoianthus*. The last is a genus of de Candolle which included three species from Ecuador

As early as 1830, Lessing realized that all the South American members of this alliance belonged to the same genus and united them under *Perezia*. However, his treatment of the genus was not taken up by any botanist except Weddell (1855) until Bentham and Hooker (1873) followed it in the *Genera Plantarum*.

Bentham (1873) went even further than Lessing and placed all of the North American species of the genus *Acourtia* into *Perezia*. Asa Gray (1883, 1884) followed the generic circumscription of Bentham and Hooker, but divided the genus into two sections: sect. *Perezia* (*Euperezia* of Gray) in South America and sect. *Acourtia* in North and Central America. After the influential works of Bentham and Hooker and of Gray, the circumscription of *Perezia* remained constant. The only changes involved the addition of new species as they were described.

There has never been a thorough, systematic study of the genus, but several local floristic treatments of the South American species are available (e.g., Perú, Tovar, 1955; Perú and Bolivia, Weddell, 1855; Paraguay-Brazil-Uruguay, Baker, 1884; Argentina, Cabrera, 1939; Chile, Reiche, 1905).

Rimo Bacigalupi published a revision of the North American section *Acourtia* in 1931 which included a detailed history of the genus, emphasizing the species of that section. The reader is referred to that study because Bacigalupi's presentation needs no

elaboration, and because the present work is concerned with the South American species of sect. *Perezia*.

GENERIC RELATIONSHIPS

The *Nassauviinae* is the extratropical, predominantly Southern Hemisphere subtribe of the tribe *Mutisieae*, to which *Perezia* belongs. Since this subtribe has been so little studied, a brief look at its constituent genera and their relationships might help to place *Perezia* in a more complete frame of reference.

Historical Treatment. A nucleus of the genera now placed in the *Nassauviinae* were first grouped by Lagasca (1811) as the first "section" in his "order" *Chaenanthophorae*. The presence of all bilabiate corollas and tailed anther appendages were his diagnostic characters for the section.

Cassini (1817) also considered that this group of genera constituted a natural assemblage, and he first applied the name "Nassauvieae" to it. However, it was not until 1821 that Cassini formally circumscribed the group as a tribe. Cassini considered the bilabiate corollas and the tailed anthers to be important tribal characters as did Lagasca, but he stressed the truncated style branches as the single most unifying character. Cassini's circumscription is essentially that which is recognized today, although it has been considered a subtribe since its rank was changed by Bentham in 1873.

In addition to making the *Nassauviinae* a subtribe of the *Mutisieae*, Bentham greatly reduced the number of genera recognized by Cassini, and even went as far as to place *Cleanthes* D. Don in synonymy with *Trixis* R. Br., a taxonomic judgment for which I can see no basis. Bentham's main guides to relationships within the *Nassauviinae* were that *Nassauvia* was closely allied to *Triptilion*, and that *Proustia* (which he replaced in the subtribe) was close to *Perezia*. *Macrachaenium* and *Leucheria* were placed first in his scheme because they most closely resembled *Chaptalia*, a genus in the less specialized mutisid subtribe *Gerberineae*. Bentham also mentioned the similarity of some genera of the *Nassauviinae* to members of the *Senecioneae*, but he did not suggest that the latter tribe was more primitive than the *Mutisieae*.

Small (1919) rarely discussed the relationships of the genera

within the different tribes of the *Compositae* because he was primarily concerned with the phylogeny of the tribes themselves. In his evolutionary scheme of the *Mutisieae*, however, he did consider the *Nassauviinae* the basal, or most primitive, subtribe. In addition, he considered *Trixis* to be the least specialized of any genus in the *Mutisieae*, a view which has since been shown to be completely incorrect (Carlquist, 1957).

Hoffmann's treatment in *Die natürlichen Pflanzenfamilien* (1893) did little to improve the taxonomy of the subtribe. Like Cassini, he excluded *Proustia* from the *Nassauviinae* solely on the basis of its round style-branch tips. However, he did recognize *Cleanthes* as a genus distinct from *Trixis*. His arrangement of the genera in the subtribe seems in no way to reflect a phylogenetic ordering, but rather follows the order in which he separated the genera in his key.

The first modern attempt to assess the relationships within the *Nassauviinae* was in a study by Wodehouse (1929a). On the basis of pollen morphology, Wodehouse concluded that *Proustia* did indeed belong in the *Nassauviinae* and was closely related to *Perezia*. The pollen evidence also indicated to him that both *Trixis* and *Jungia* were isolated genera in the tribe. *Nassauvia* and *Triptilion* are similar to one another palynologically as they are morphologically. Wodehouse treated the remaining genera as a rather loose assemblage in which it was hard to determine relationships on the basis of pollen morphology. In contrast to Small (1919), Wodehouse (1929a) concluded that the genus *Trixis* represented the culmination of a phylogenetic trend in the *Mutisieae*.

Discussion. Because of the conflicting opinions of former authors, I have made a preliminary study of the different genera in the *Nassauviinae*. My conclusion is that Bentham (1873) and Wodehouse (1929a) were justified in including *Proustia* in the *Nassauviinae*. It is considered to be closely allied to *Perezia*, especially to the section *Acourtia*. On the basis of habit, anatomy, morphology, and cytology, it appears that *Proustia* and *Perezia* section *Acourtia* are more similar to one another than the two sections of *Perezia* are to each other. However, alteration of the present circumscription of *Perezia* must await further study. The following morphological similarities of *Proustia* to the genera of the *Nassauviinae*, and *Perezia* sect. *Acourtia* in particular, should

be noted. Although *Proustia* does have rounded rather than truncate style-branch tips, it has the same type of anther tails, terminal anther appendages, and homomorphic capitula of bilabiate florets, unique to the *Nassauviinae*. There is a tendency for the style-branch tips of some nassauvid species to appear rounded (e.g., *Perezia nutans*) indicating that the apex shape of the stylar branches may have been overemphasized in the past as a character for separating higher categories. The habit of some species of *Proustia* is also very similar to that of various species of *Trixis* and *Perezia* sect. *Acourtia*. A particular type of brown "wool" occurs in the leaf axils and on the caudices of both *Proustia* and *Perezia* sect. *Acourtia*, but never on any parts of the plants of *Perezia* sect. *Perezia*. Finally, the pappus, while normally setose in both *Perezia* and *Proustia*, has a tendency in some species of *Perezia* sect. *Acourtia* and *Proustia* to become thickened at the apex of individual bristles.

A few other personal observations about the subtribal taxonomy might be mentioned. First, *Cleanthes* should be kept distinct from *Trixis* as in Hoffmann's treatment; second, the monotypic genus *Ameghinoa*, described in 1897 after the works of Bentham and Hooker (1873) and Hoffmann (1893), is placed in synonymy with *Trixis*. The gross morphology and pollen shape indicate that *A. patagonica* is merely a specialized *Trixis*.

The position of another monotypic genus, *Cephalopappus* Nees & Mart. is particularly hard to determine because it is apparently very rare, and the original description and accompanying illustration are confusing. I have not seen a specimen of this species and therefore it is impossible to comment on its affinities.

On the basis of this preliminary survey of the subtribe, it would be presumptuous to attempt to draw positive lines of relationships between the different genera. There are undoubtedly several distinct evolutionary lines within the *Nassauviinae*, and obviously there has been considerable mosaic evolution. The subtribe appears to contain a natural group of genera (except perhaps for *Cephalopappus* and *Leunisia*) which arose from a common ancestral stock, and which can be grouped into clusters of genera. Future detailed anatomical, morphological and cytological work should refine the relationships within each of these.

As noted by many workers who have dealt with the *Nassauviinae*, *Nassauvia* and *Triptilion* constitute a very closely related

unit within the subtribe. *Jungia* (incl. *Pleocarpus*) stands somewhat isolated in the subtribe and is more similar to *Trixis* than to most of the other genera. *Leunisia* is an even more isolated genus, but again shows some slight resemblances to *Trixis*. *Leucheria* and *Perezia* sect. *Perezia* appear to be related and both are morphologically somewhat in the middle of the remaining genera because of their inclusion of such a wide spectrum of types. Both contain species that are small, monocephalous and scapose, and species that are robust, tall, leafy, having polycephalous flowering stems. Genera such as *Macrachaenium* are similar in morphology to the scapose species of these two genera whereas *Polyachyrus, Cleanthes, Pamphalea,* and *Mosharia* are most similar to the cauline, polycephalous species.

KEY TO THE GENERA OF SUBTRIBE NASSAUVIINAE

A. Capitula with 2–5 florets, (B).
  B. Capitula with two dimorphic florets, ... *Polyachyrus* Lag.
  B. Capitula with 4–5 monomorphic florets, (C).
    C. Pappus simple (entire), paleaceous, lanceolate, usually more than 3 bristles per floret ..... *Nassauvia* Juss.
    C. Pappus paleaceous, feathery at the apex or oblanceolate, 3 pappus bristles per floret ..... *Triptilion* Ruiz & Pav.

A. Capitula with more than 6 florets per capitulum, (D).
  D. Receptacle with numerous paleae, (E).
    E. Paleae a narrow cylinder enclosing each floret ..... *Jungia* L. f.
    E. Paleae of the outer florets a cup-like structure around the ovary ..... *Moscharia* Ruiz & Pav.
  D. Receptacle without paleae or with only a few scattered at the margins of the receptacle, (F).
    F. Plants covered with woolly or silky white trichomes, (G).
      G. Leaves reduced to three-parted spines .... *Oxyphyllum* Phil.
      G. Leaf blades flat, without sharp spines, (H).
        H. Leaves with extremely long petioles, pappus fine, silky, dirty-yellow ..... *Macrachaenium* Hook. f.
        H. Leaves shortly petioled or attenuate at the base, pappus setose, plumose, or lacking, (I).
          I. Florets densely pubescent, pappus completely lacking ..... *Cephalopappus* Nees & Mart.
          I. Florets glabrous, pappus setose or plumose ..... *Leucheria* Lag.
    F. Plants glabrous or with scattered multicellular glandular trichomes. Woolly trichomes sometimes present in the leaf axils or on the caudex, (J).
      J. Involucral bracts narrowly lanceolate, yellow-green, outer and inner equal in length; florets bright yellow, (K).
        K. Achenes with glandular trichomes with a prominent, bulbous apex, clear in color ..... *Leunisia* Phil.
        K. Achenes with glandular trichomes without a swollen apex

..... *Trixis* R. Br. (including *Ameghinoa* Speg.)

J. Bracts pale green, dark green, or reddish, often scarious along the margins, outer frequently shorter than the inner; florets blue, white, or pink (pale yellow in some species of *Perezia*), (L).

L. Pappus absent ..... *Pamphalea* Lag.

L. Pappus present, (M).

M. Style-branch tips rounded ..... *Proustia* Lag.

M. Style-branch tips truncate, (N).

N. Rows of involucral bracts in three or fewer series; capitula very hemispherical; achenes densely pubescent; caudex glabrous, (O).

O. Capitula shorter than 6 mm; pappus setose ..... *Cleanthes* D. Don.

O. Capitula longer than 6 mm; pappus tending toward, or actually, plumose .... *Leucheria* Lag.

N. Rows of involucral bracts in usually more than three series, scarious; capitula hemispherical or turbinate; tufts of brown wool often present on the caudex ..... *Perezia* Lag.

TREATMENT OF MORPHOLOGICAL CHARACTERS OF PEREZIA

To standardize data collecting from herbarium specimens, a data sheet was prepared containing recordings of all pertinent characters, both numerical and non-numerical, for over 1200 specimens. Each specimen was given a reference number when it was examined. The collector, his number, the date and place of collection and the herbarium which housed it were recorded, making it possible to relocate the specimen from its reference number. The altitude, latitude and longitude of the collection locality were also recorded. All meristic characters were measured across the broadest area for width, and down the longest part for length. The 24 numerical characters measured or counted, and the 23 non-numerical characters recorded are listed in the left-hand column of Table 1. The data were punched on IBM cards, using numbers or letters as shown in the right-hand column of Table 1.

Non-numerical characters were not given numerical values as suggested by Sokal and Sneath (1963, p. 291) or Rogers *et al.* (1967) because it was felt that such a conversion was useless. Minkoff (1965) has shown some of the dangers involved in treating non-numerical characters statistically when they are assigned arbitrary numerical values. In this case, the non-numerical characters were represented by letters facilitating the card punching and

making it easier to recall the character state for which they stood.

Using these data cards, a series of computer programs were run, designed to provide a variety of information about the specimens, populations and species. In the programs described below, the specimens were grouped into populations or species before the program was run.

The first program was a simple one, written to arrange the numerical characters in ascending order for each species. A list was printed for each character, containing the lowest to highest value of that character for the species being dealt with. The specimen reference number appeared next to the value to which it corresponded, making it possible to find the specimen having the lowest, highest, etc. value for that character. This character arrangement program was useful as an aid in writing species descriptions. Each range of measurement for a certain character in a species description represents the observed range for all specimens measured.

An advantage of the values being printed in ordered sequence is that it was possible to see immediately whether or not there was a skewed or bimodal distribution of the characters within a species. In almost every case, the characters seemed to fit a normal distribution.

The second program run was designed to find the means, standard deviations, and coefficients of variation for each character for each population of *Perezia*. Again, the specimens were pre-grouped beforehand. The purpose of this program was to find changes in the mean values of the characters from population to population within a given species, and to see whether such changes constituted a pattern in several species. These statistical procedures are standard in systematic biology (see Simpson, Roe, & Lewontin, 1960, Chapt. 6). Most of the useful information which came from this program is discussed under the species where it is pertinent. However, a few examples of the kind of information derived are given here.

It was found that a similar pattern of variation in plant size existed in three sympatric species of *Perezia (P. lyrata, P. prenanthoides,* and *P. pedicularidifolia)* which grow in the *Nothofagus* forest of southern Chile. In all species, the populations with the largest plants occurred in the area of the north-central part of the range. The average plant size in all of these species decreased

slightly in northern, and then more sharply in southern populations (Fig. 20). The part of the range in which the populations with the largest plants occurred coincided in the three cases. These findings suggest that there is an area of optimal growth conditions in the north-central part of the Valdivian forest for those species of *Perezia* adapted to the mountain slopes of the deciduous *Nothofagus* forest zone. Presumably, increased dryness in the north and increased cold in the south are influential in reducing plant size in these areas.

In addition, this program was useful for showing the overlap present in a given character for different populations of a species, and provided the statistics necessary for a *t*-test for significance of the differences. In one case, two populations of *Perezia purpurata* had been considered separate species because the head size in one was supposed to be smaller than in the other. Graphing the means and standard deviations of these and several other populations (see discussion, Part II under *P. purpurata* and Fig. 23) showed a large amount of overlap in the parameters for head size. A similar test for head length and head width was used for *P. ciliosa*.

A modification of the same program was used in the palynological study discussed below. Calculations of the means and standard deviations of the pollen grain diameters for the different species indicated that there is some consistency in grain diameter within a species group (Table 4), although the size differences between the groups were not significantly different.

A third program was run to find the correlation, *r*, between all possible pairs of characters for each species. Species were pregrouped for these runs, but in some cases subspecies or populations were also run individually to find any correlations which might have existed in large, isolated populations. The significant probabilities for the correlation coefficients were taken from Table V of Simpson, Roe, and Lewontin (1960) and those correlations found to be significant at the .05, .01, and .001 levels were noted for further analysis.

Correlation coefficients were also computed between meristic characters and altitude, latitude, and longitude. In general, very few statistically significant correlations were found between the numerical characters and any of the three geographical parameters. The apparent absence of altitudinal effect could be due

TABLE 1. GROSS MORPHOLOGICAL CHARACTERS OF PEREZIA RECORDED[1]

NUMERICAL CHARACTERS

Character	*Order of Magnitude*
Specimen number	1–1500
Altitude	0–9000
Latitude	–6–60
Longitude	50–80
Height of plant	1–99
Height of peduncle	1–99
Number of stem leaves	0–99
Width of head	4.5–.5
Length of head	4.5–.5
Width of involucre	4.5–.5
Length of involucre	4.5–.5
Number of heads per peduncle	1–99
Number of heads per plant	1–99
Width of basal leaf	13.0–.1
Length of basal leaf	33.0–.3
Number of rows of bracts	1–7
Width of outer bract	1.5–.1
Length of outer bract	2.0–.1
Width of inner bract	2.0–.1
Length of inner bract	4.0–.9
Percent scarious of outer bract	0–99
Percent scarious of inner bract	0–99
Length of floret excluding ovary	4.5–.5
Length of outer ligule	.5–.1
Length of pappus	3.0–.5
Number of florets per head	9–82

NON-NUMERICAL CHARACTERS

Color of corolla	blue, white, violet, yellow, red, orange, mauve, magenta, pink, cream (B, W, V, Y, R, O, U, M, P, C)
Description of stem leaf shape	lanceolate, needle-like, scale-like, lyrate, ovate, spathulate, absent (L, N, S, Y, O, P, A)
Description of stem leaf margin	entire, ciliate, serrate, dentate, pectinate (E, C, S, D, P)
Description of stem leaf size	small (less than 3 cm), large (greater than 3 cm), absent (S, L, A)

[1] NOTE: If a character could not be determined for a specimen, the space for that character was left blank. A value of zero on an IBM card meant that the value for a character was zero. Two IBM cards were used for each specimen of *Perezia* examined. The order given here is not the order in which the data were actually punched on the data cards, but is the order of a set of rearranged data cards punched by the computer. In the case of numerical characters, all measurements are in centimeters except altitude (in meters) and latitude and longitude (in degrees and fractions of degrees; minus degrees for north latitude). In the case of non-numerical characters, the letters in parentheses were punched on the cards.

NON-NUMERICAL CHARACTERS *(cont'd)*

Shape of involucre	turbinate, hemispherical, cup (T, B, C)
Direction of head	upright, nodding (U, N)
Shape of basal leaf	spathulate, lanceolate, lyrate, linear, ovate, linear-lanceolate, oblanceolate, obovate (SP, LA, LY, LI, OV, LL, OL, OB)
Edge of basal leaf	entire, ciliate, spiny, parted-entire, parted-dentate, parted-doubly divided, dentate, serrate, undulate, lobed (EN, CI, SP, PE, PS, PD, DE, SE, UN, LO)
Surface of outer bract	glandular trichomes, punctate glabrous (G, P, A)
Surface of inner bract	"
Surface of peduncle	"
Surface of basal leaf	"
Shape of outer bract	linear, lanceolate, ovate, oblong, pandurate, spathulate, circular, reniform, oblanceolate (LI, LA, OV, OB, PA, SP, CI, RE, OL)
Tip of outer bract	acute, obtuse, mucronate, acuminate (A, O, M, N)
Edge of outer bract	pectinate, dentate, serrate, ciliate, entire, undulate, (PT, DE, SE, CI, EN, UN)
Surface of achene	glandular trichomes, double hairs, two kinds of trichomes, glabrous (G, S, D, A)
Amount of achenal pubescence	slight, dense, absent (S, D, A)
Color of achenal pubescence	copper, blond, white, absent (C, B, W, A)
Description of receptacle	ridged, glandular trichomes, long trichomes, glabrous (R, G, T, A)
Amount of receptacular pubescence	dense, slight, absent (D, S, A)

in part to the fact that limited elevation data were available. In addition, species of *Perezia* usually grow at fairly constant altitudes throughout their ranges. The lack of significant correlations between characters and latitude or longitude might result from the fact that only linear correlations are found using *r*. For example, the type of variation seen in the three *Nothofagus* forest species discussed above was not detected using the standard correlation coefficient.

An exception to the general lack of correlation between geography and numerical characters was found in *Perezia multiflora*. Significant correlations were found between both longitude and

altitude and capitula length and width, leaf length, and the number of heads per peduncle. The correlations indicate that there is a cline in these morphological characters from the high northwestern part of the range to the low southeastern part. These correlations, with respect to the interpretation of the subspecies of *P. multiflora,* are discussed fully under that species.

The use of correlations also emphasized the need, in some cases, to examine the size of an organ or part of a plant in the context of the entire plant. A group of populations included here in *Perezia lyrata* were previously considered to be a separate species because they had "larger capitula and larger outer bracts." An analysis of the correlations showed that the larger capitula and bracts were correlated with an overall increase in plant size and merely represented one extreme of variation present in the species.

MORPHOLOGY AND ANATOMY

Habit. In both sections of *Perezia,* all species are perennial herbs although some species of sect. *Perezia* have been mistakenly described as annuals. The most common habit of the South American species is a rosette with one monocephalous flowering stem but there is considerable variation of this basic type within the section. However, habit is quite constant within a species group, making it a useful taxonomic character. The habit of a species is also correlated with its ecology and, it should be noted, related species of a group tend to grow in the same, or very similar habitats (Table 2).

There are five basic types of habit present in the South American *Perezia.* One includes tall, leafy plants with branched flowering stems and numerous capitula (PLATE 1–4). This growth form is found in both the *P. multiflora* and the *P. prenanthoides* species groups. In this case, the similarity of habit appears to reflect the retention of a primitive character from an ancient, rather than recent, common stock.

Another habit type, common to the members of the *Perezia magellanica* species group, is a fairly compact basal rosette with one or several monocephalous flowering stems. Plants of this group grow singly in, or around, rock crevices (PLATE 1–5) where they receive protection from the cold and wind.

TABLE 2.

CORRESPONDENCE BETWEEN HABIT, HABITAT, AND SPECIES GROUPS

	ANDES						LOWLANDS		
	Central			*Southern*		*Patagonia*			
	Tall grass — montane slopes	Dry, rocky scrub — high slopes	Short grass — high peaks	*Nothofagus* forest	"Alpine" meadows — mountain peaks	Magellanic moorland	Dry grass and scrub steppe	Paraguay-Brazil-Uruguay open woods and grasslands	
P. multiflora		L	L					L	
P. squarrosa								L	
P. kingii								L	
P. prenanthoides				L					
P. nutans				L					
P. pungens	L–A								
P. ciliaris		L							
P. carduncelloides	L								
P. sublyrata			A						
P. mandonii	A								
P. ciliosa			A						
P. purpurata		A							
P. pilifera		R							
P. carthamoides		A							
P. viscosa						A			
P. lactucoides							A		
P. pedicularidifolia						A			
P. lyrata						A			
P. fonkii						A			
P. delicata						A			
P. magellanica							A		
P. calophylla						A			
P. bellidifolia						A			
P. megalantha						A			
P. coerulescens			R						
P. pinnatifida	R								
P. pygmaea	R								
P. poeppigii	A–C								
P. linearis				C					
P. recurvata							C		

L = large, caulescent, many-headed plants
A = open rosette, usually one head/stem
R = tight, small rosette
C = cushion plant

All of the members of the *Perezia pungens* group share a third, and the most common, habit type which is essentially a larger, more open form of the rosette found in the *P. magellanica* group. However, associated with this loose rosette are numerous flowering or slightly branched stems with several capitula.

The fourth type of habit is the other extreme aspect possible for a rosette plant, i.e., a very reduced, compact rosette closely appressed to the ground (PLATE 2). Species with this type of habit belong to the *Perezia coerulescens* complex and frequently form mats of numerous plants crowded together at very high elevations.

The last general habit type is restricted to the *Perezia recurvata* group which occurs in Patagonia. There is a tendency in the species of this group for plants to branch at the base and form a cushion type of aspect (PLATE 2–4).

Although there is overlap in the different types of habit, the growth form of a species usually allows it to be placed readily into one of the species groups (Table 2). Often, the aspect of a specimen combined with one other important character, such as leaf shape or bract morphology, is all that is needed to identify a species.

Roots and Rhizomes. All species of *Perezia* sect. *Perezia* have rhizomatous rootstocks except those of the *P. multiflora* species group, the three members of which have long taproots. Although woolly caudices and tuberous roots occur in the North American species, neither is found in sect. *Perezia*.

Foliage. The basal leaves in species of *Perezia* vary in shape from broadly ovate to linear, sessile to petioled, and from entire to deeply and doubly lacerate. The shape, margin, and the base of the leaf are very useful in separating species.

Although the leaf shape and margin are usually consistent within a species, *Perezia pilifera* exhibits a dimorphism for leaf shape. Most plants have fleshy, highly segmented leaves, each segment of which is terminated by a long, soft, white spine. Some plants, however, have entire linear leaves which are three-angled in cross section. These needle-like leaves sometimes have long white spines along the margins, and invariably are terminated by one. Individual plants are always composed of only one leaf type, and frequently all of the plants within one population have the same leaf type. Until now, the two forms of *P. pilifera* were placed in

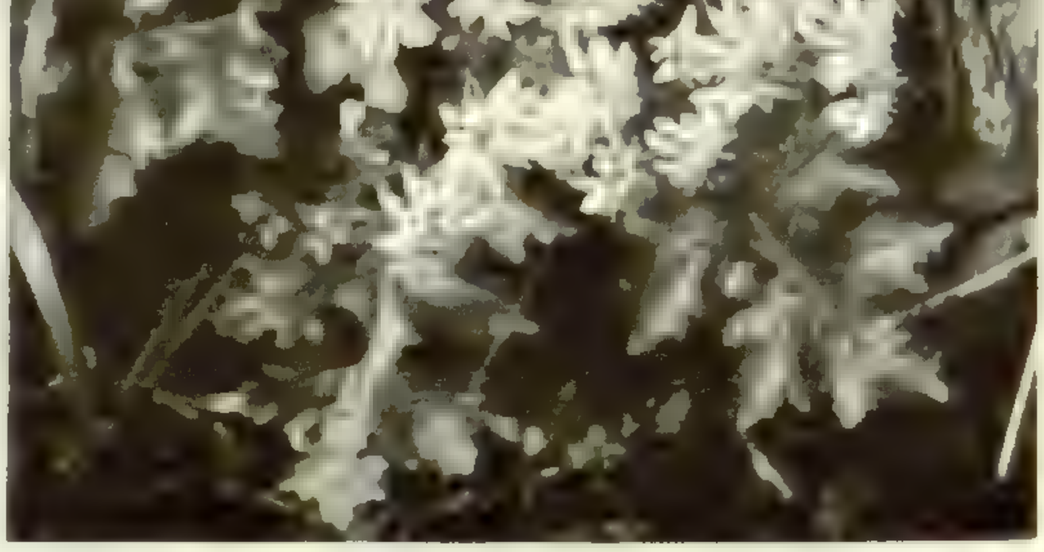


PLATE 1. FIG. 1–1 to 1–3: Capitula of the three closely related species of the *Perezia pungens* complex showing differences in the involucral bracts. 1–1. *P. pungens*. 1–2. *P. ciliaris*. 1–3. *P. carduncelloides*. All natural size. FIG. 1–4, 1–5: Habit of two species. 1–4. *P. prenanthoides*. 1–5. *P. lyrata*. Both reduced about 10 ×.

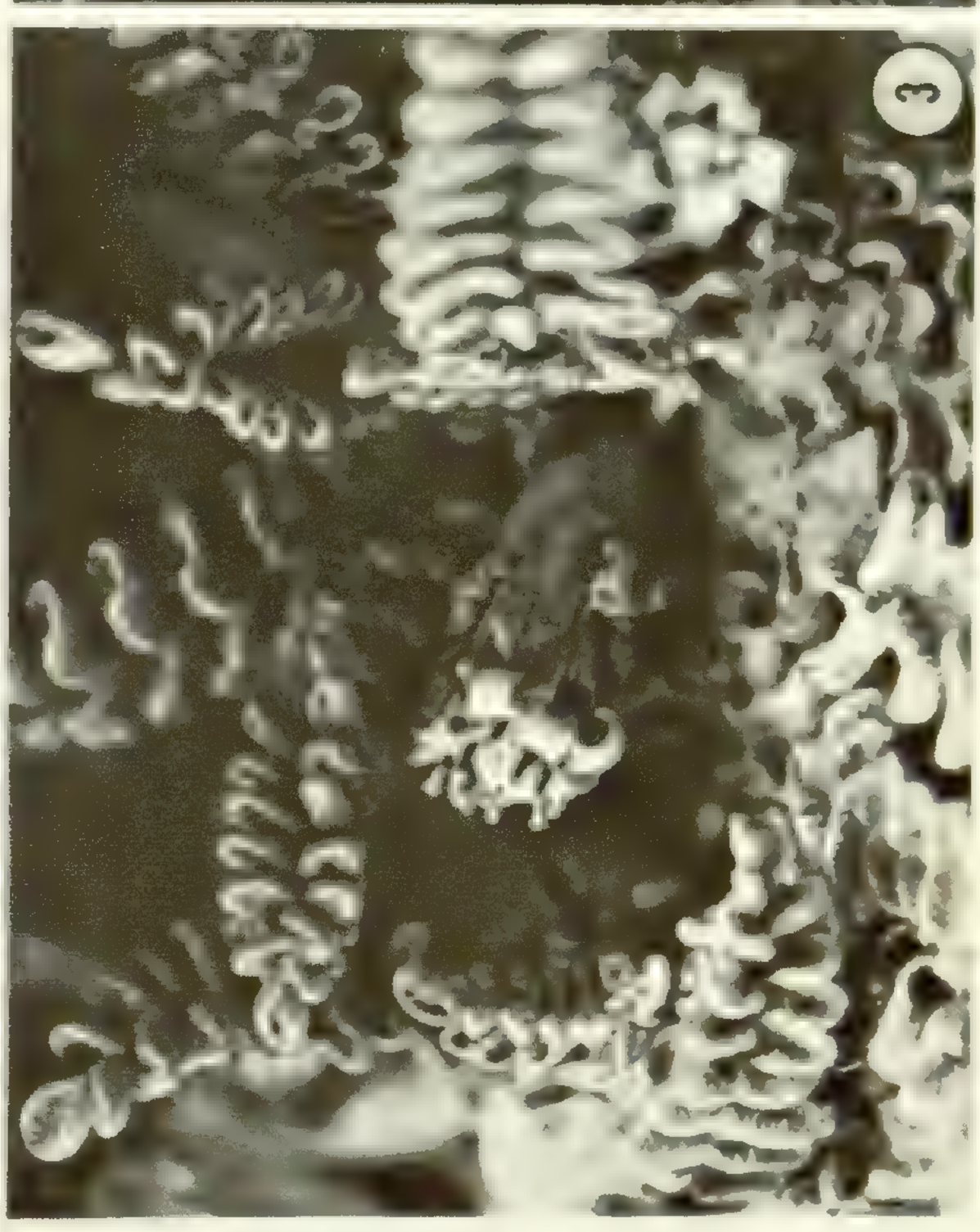


PLATE 2. FIG. 2–1 to 2–3. The three closely related members of the *Perezia coerulescens* complex: 2–1. *P. coerulescens* (1/5 ×); 2–2. *P. pygmaea* (3/4 ×); 2–3. *P. pinnatifida* (about natural size). FIG. 2–4. Cushion plant habit of *P. recurvata* (ca. 1/12 ×).

different species. In Bariloche, Rio Negro, Argentina, I found a population with both types of plants, even though the dissected leaf form was the more prevalent. Since intermediate leaf types do not occur, it is possible that the leaf shape is controlled by a relatively simple genetic mechanism, and the presence of homogeneous populations (only one form present) could be due to establishment by a propagule with alleles for only one form. This type of colonization corresponds to the founder principle of Mayr (1963).

A second species, *Perezia recurvata,* has three more or less recognizable leaf types present in various populations. In this case, intermediate leaf types are common and variation is almost continuous as shown in Fig. 28 and 29. The partial correlation of leaf type with geographical area (Fig. 27–4), and the presence of intermediates indicate that the present variation reflects former isolation, subsequent secondary contact, and recent gene flow. It appears that morphological changes, but not reproductive isolation, occurred during periods of separation.

Clearings were made of the leaves of all species of *Perezia* sect. *Perezia* to determine the kind(s) of stomata, their distribution, the vascular patterns, and the types of trichomes. Preparations were made using the standard procedure of clearing in 1 per cent NaOH for 24 hours, dehydrating in a graded alcohol series, staining in basic fuchsin, and placing in permount.

All of the species except two were found to have ranunculaceous stomata liberally distributed over both leaf surfaces. Two species, *Perezia linearis* and *P. recurvata,* had stomata only in two narrow bands on the underside of the leaf next to the midrib. This reduction in the number of stomata is presumably correlated with the xerophytic conditions of the Patagonian lowlands where the two species occur. Pyykkö (1966) found a similar sort of stomatal restriction in species of other genera adapted to the Patagonian steppe.

The leaf venation of all species investigated is basically reticulate, but in some species such as *Perezia pilifera* and *P. recurvata* it is so reduced as to appear open. This open venation appears to be correlated with specializations for a xerophytic habitat. A similar situation was reported in *Raoulia* Hook. f. by Solbrig (1960). The venation pattern is not constant within one species, and in *P. pungens* and *P. multiflora* it can vary from densely

reticulate to almost open, depending on the ecology of the population.

Foliar trichomes vary considerably in type, size, and density in different species of *Perezia*. No species has completely glabrous leaves although some species such as *P. bellidifolia* and *P. lactucoides* appear glabrous unless carefully examined.

Involucral Bracts. Bacigalupi (1931), in his treatment of the North American species of *Perezia*, correctly stated that the involucral bracts were one of the most diagnostic characters in the genus. The bracts are free and arranged in several series increasing in size (generally) from the outside to the inside. The outer and the inner bracts vary considerably in morphology and are treated separately here although the intermediate series are transitional in size and shape.

The specific characters of the species are primarily in the morphology of the outer bracts which differ in shape, margin, pubescence, color, and number. The outer series can range in morphology from stiff lanceolate, very sclerenchymatous and scarious bracts in one species, to soft, foliaceous, and non-scarious bracts in another. The margins vary interspecifically from entire to dentate or pectinate, and the apex from mucronate to obtuse. The inner bracts are consistently lanceolate with scarious margins.

Capitula. The majority of the South American *Perezia* have monocephalous flowering stems which may, or may not, be scapose. Species with polycephalous flowering stems may have the heads arranged in racemes or panicles. Where there is a branched, flowering stem, flowering begins with the topmost (innermost) capitulum and proceeds downward (outward). In two species, *P. nutans* and *P. multiflora*, it appears that some heads never mature. Individual heads are upright in most species, but are nodding in a few.

The capitula of all South American species appear radiate because the ligules of the outer florets are longer than those of the inner florets. The amount of difference between the lengths of the outer and inner ligules varies in the different species. The capitula of *Perezia magellanica* are very radiate in form, whereas in other species they are barely so. Without exception, flowering within a head proceeds from the outside to the inside.

Florets. As in most genera of the *Nassauviinae*, the florets of *Perezia* are bilabiate with the outer three petals fused into a

tridentate ligule and the inner two petals free and curled. Blue is the most common corolla color and is found in 87 per cent of the species (26 of 30 species). Other colors, ranging from brown through crimson, magenta, pink, cream, white, and yellow also occur, and frequently several floret colors can be found on different plants of the same species.

The corolla tube and ligule of all the florets in a head are monochromatic in the species of *Perezia* sect. *Perezia* except *P. multiflora*. The ligule and the outer half of the corolla tube are either blue or white in this species and the inner two petals and inner half of the corolla tube are yellow. The effect of this dichromatic pattern is to give the capitulum the appearance of having blue (or white) ray florets and yellow disc florets.

A few species, especially in the *Perezia magellanica* and the *P. pungens* alliances, have glandular trichomes on the corolla tube near the throat and on the ligule. In a few cases, the presence or absence of these floral trichomes has proved useful in separating species.

The anthers of all species of *Perezia* have tails and terminal appendages like other members of the *Nassauviinae*. A brief survey of the comparative lengths of the anther tails in the various species of *Perezia* indicated that there were no meaningful size differences between species. Frequently, it has been noted that the anthers are brightly colored and form a contrast with the corolla. Bright deep blue, black, malachite green and pink anthers have been recorded by various collectors.

The styles always have globose bases, terete stems, and recurved truncate style branches. In some cases, as in a few specimens of *Perezia nutans*, the style branches were observed to be rounded and to approach the type found in *Proustia*. The styles are usually yellow, but blue and pink ones have also been recorded.

Small (1919) recorded that there was a mechanism for explosive dehiscence in *Perezia multiflora*. However, I have never noticed an explosive reaction upon touching florets of *P. multiflora* in the field. A few flowers of several species of *Perezia* have been found which had styles with three stigma branches. It has been noted that such abnormalities occur sporadically throughout the *Compositae* (Bentham, 1873; Small, 1919) and seem to be teratological cases of no evolutionary or taxonomic importance.

Pappus and Achenes. A setose pappus is present in all species of the genus, varying in color from white to deep red-brown.

The achenes are uniformly ellipsoidal in shape and inconspicuously ribbed. Their surface is generally pubescent and the trichome type is frequently distinctive enough to allow determination of the species group (Fig. 3, Table 3) but nothing more. The density of the achenial hairs is variable within a species and therefore unreliable as a character for the separation of species.

Receptacles. The receptacles of the species of *Perezia* are of two types, fimbrillate and foveolate with a few scattered trichomes on the surface. When the receptacle is fimbrillate, tufts of long silky trichomes arise from around the points of achene attachment. These tufts of trichomes are usually associated with achenes covered with double hairs. The glabrous foveolate receptacles are usually found in species with glandularly pubescent or glabrous achenes. The receptacle type, therefore, shows the same correlations with species groups as does the achene pubescence type (Table 3).

Trichomes. The types of trichomes found on plants of *Perezia* species fall into two broad categories: the double hairs or *Zwillingshaare* of Hess (1938) (Fig. 3–1 to 3–3), and glandular tri-

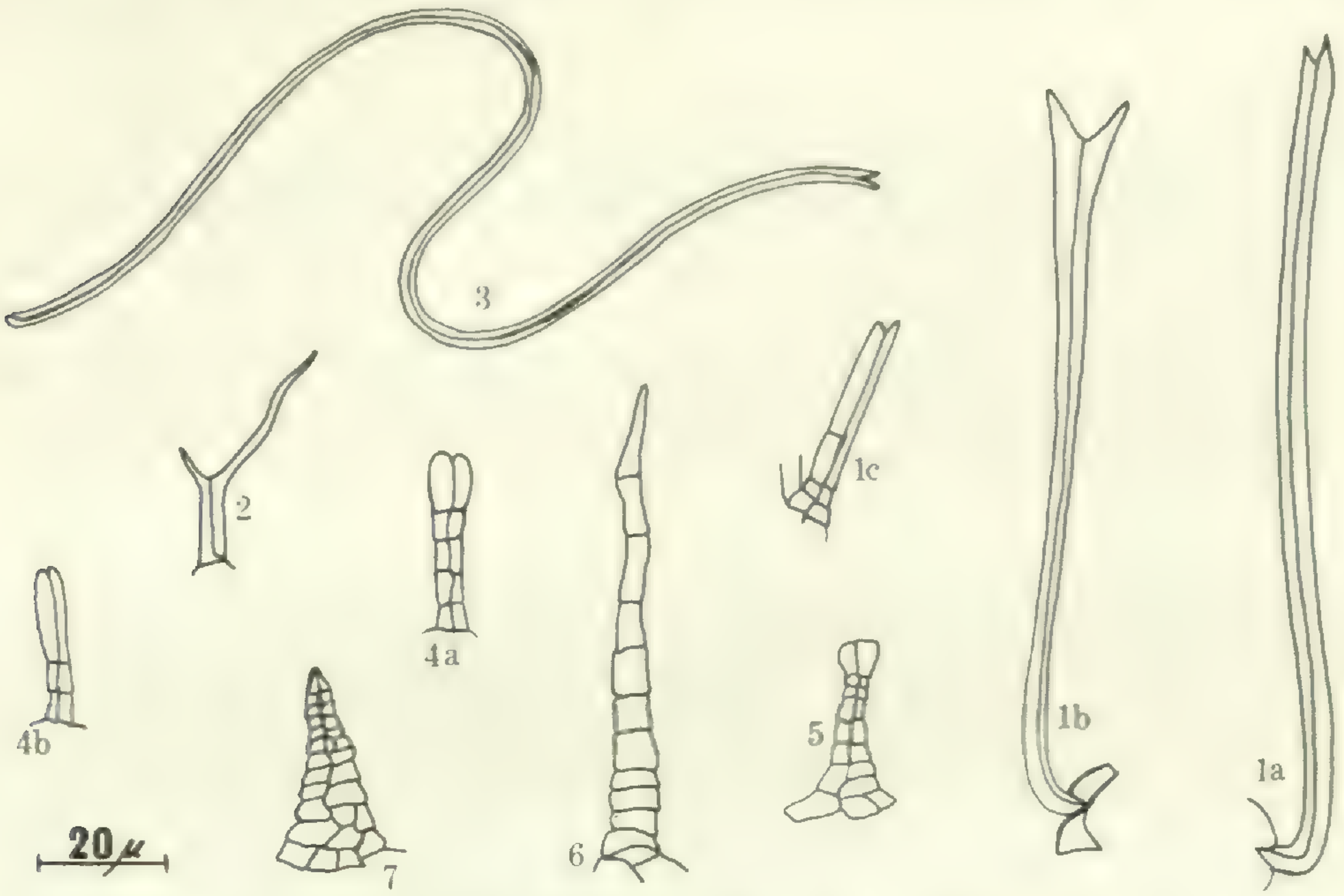


FIG. 3. Trichome types of species of *Perezia* sect. *Perezia*. Types 3–1 to 3–4 are achenial trichomes, types 3–5 to 3–7 are foliar trichomes. Trichomes 3–1 to 3–3 are "double hairs" and 3–4 to 3–7 are glandular hairs.

TABLE 3. TRICHOME TYPES OF PEREZIA SPECIES[1]

	ACHENIAL TRICHOMES					GLANDULAR TRICHOMES		FOLIAR TRICHOMES		
	1a	1b	1c	2	3	4a	4b	5	6	7
P. multiflora	D							M–D		S
P. squarrosa	D							S		S
P. kingii	D							S		S
P. prenanthoides							D	M		
P. nutans							D	M		
P. pungens			S–M					S–D		
P. ciliaris							S			
P. carduncelloides							M	M		
P. sublyrata	S						M–D	S–M		
P. mandonii	S						S	S		
P. ciliosa	D							S		
P. purpurata	S–D						S–D	S–D		
P. pilifera					D			S		
P. carthamoides	M–D						S–M	S–M		
P. viscosa	D							D		
P. lactucoides	M							S		
P. pedicularidifolia	D						S–M	M		
P. lyrata	D						S–D	S–M		
P. fonkii	D							M		
P. delicata	D							S		
P. magellanica	D									D
P. calophylla	D							D		
P. bellidifolia	D							S		
P. megalantha	D							D		D
P. coerulescens	S		S			S		S–D		
P. pinnatifida	S							D		
P. pygmaea	S						M–D	S		
P. poeppigii	M			S				S		
P. linearis	M			S				S		
P. recurvata	M			M				S		

[1] Trichome types are illustrated in Fig. 3.
Symbols: S = slight, M = moderate amounts, D = dense

chomes (Fig. 3–4 to 3–7). The double hairs are found on only the achenes and the receptacles, and vary from copper to white in color. The double hairs of the achenes have a specialized basal cell which is hygroscopic and is important for the fuctioning of the trichomes. The double hairs on the receptacle do not have a special cell at the base.

According to Hess (1938) the double hairs have several functions: they aid in dispersal by acting as a second pappus; they help to protect the achene from climatic and mechanical damage;

they help to secure the achene to the substrate upon which it falls; and they aid in the uptake of water. Hess postulated that double hairs were the primitive achene trichome type in the *Compositae*, and that substitution of another type of trichome, or loss of all hairs, represented advanced conditions.

Within *Perezia*, Hess' generalization appears to be true, as those species which are most specialized in habit and morphology are usually those with reduced amounts of double hairs, glandular rather than double hairs, or glabrous achenes. This does not mean that a species with dense double hairs on its achenes is necessarily primitive. In *Perezia*, as in all organisms, evolution is reticulate, and different characters evolve at independent rates. Whether or not a species is primitive or advanced can be determined only by taking all of its characters into account.

Glandular trichomes are found on all parts of the plant body, but vary greatly in size and density. Their function, in addition to their generalized secretory ability (Metcalfe & Chalk, 1965; p. 783), has not been determined (at least in the *Compositae*) and, as a result, it is difficult to ascertain the reasons for increases or decreases in the densities of glandular trichomes. From specimens alone, it appears that changes in the amounts of foliar trichomes of *Perezia* are ecologically controlled and highly unreliable as a taxonomic character.

The glandular trichomes of a few species contain a reddish pigment which gives the bracts and stems on which they occur a red-purple cast. Marked quantities of these pigment-bearing trichomes have been found only in *Perezia magellanica* and *P. pedicularidifolia*. The red color of the bracts of other species is due to pigmentation of the epidermal, rather than trichome, cells.

Drawings of the different types of achenial and foliar trichomes are given in Fig. 3. Table 3 lists the various kinds of trichomes found in the different species of *Perezia*. It is evident from this table that certain types are correlated with the groupings of species arrived at by the use of gross morphological characters. Although to a lesser extent, the foliar trichome types are also indicative of affinities between species (Table 3). The profitable use of trichomes in *Perezia* corroborates the conclusion of Drury and Watson (1965, 1966) that trichomes should be more widely and critically examined in systematic studies.

An investigation of its trichomes was a major factor leading

to the exclusion of *Perezia lanigera* from this genus. It has a completely different type of achenial trichome from any species of *Perezia* and it also has tufts of dense, woolly hairs in the leaf axils. Axillary trichomes have not been found in any South American species of *Perezia*.

DISTRIBUTION AND ECOLOGY

Habitats. Twenty-seven of the 30 species of *Perezia* sect. *Perezia* are Andean, and 23 of these grow above timberline. The three extra-Andean species (one of which has a subspecies in the Andes) are centered in the open woods of the Paraguay-Uruguay-Brazil lowlands. The Andes themselves are covered by several major kinds of vegetation as shown in Fig. 4, each comprised of numerous microhabitats. Species of *Perezia* have radiated into almost every habitat now present along the Cordillera. A species is frequently limited in distribution by its habitat, and has a growth form correlated with it. Some relationships between habitat, habit, and species groups are given in Table 2.

The high Andean chain above timberline is usually divided into two gross vegetation types: the humid, lush, páramo of Venezuela, Colombia, and Ecuador; and the dry, relatively barren puna to the south. The boundary between these two major zones is the northern distributional limit of the South American *Perezia* (compare Fig. 2 with Fig. 4), although two species, *P. multiflora* and *P. pungens*, encroach upon the páramo in Ecuador and extreme southern Colombia. The puna, where the majority of the species of *Perezia* are located, is actually a composite of arid valleys, grassy peaks, shrubby and thorny slopes, volcanic cones, and the windswept steppe of the altiplano (Fig. 4). In the south, beginning at about latitude 40°S, the peaks are covered with more humid, almost alpine, meadows.

Two endemic species are found in the *Nothofagus*, or southern beech forest, in the southwestern part of the continent along the montane slopes. Several other species of *Perezia* grow into the forest, but are also found in open areas and along the forest edge. East of the southern Andes is the barren grass and scrub of Patagonia. Only one species is actually found on the Patagonian steppe, although a few others stray onto its western edge. Figure 4 also shows the Magellanic moorland at the extreme tip of the

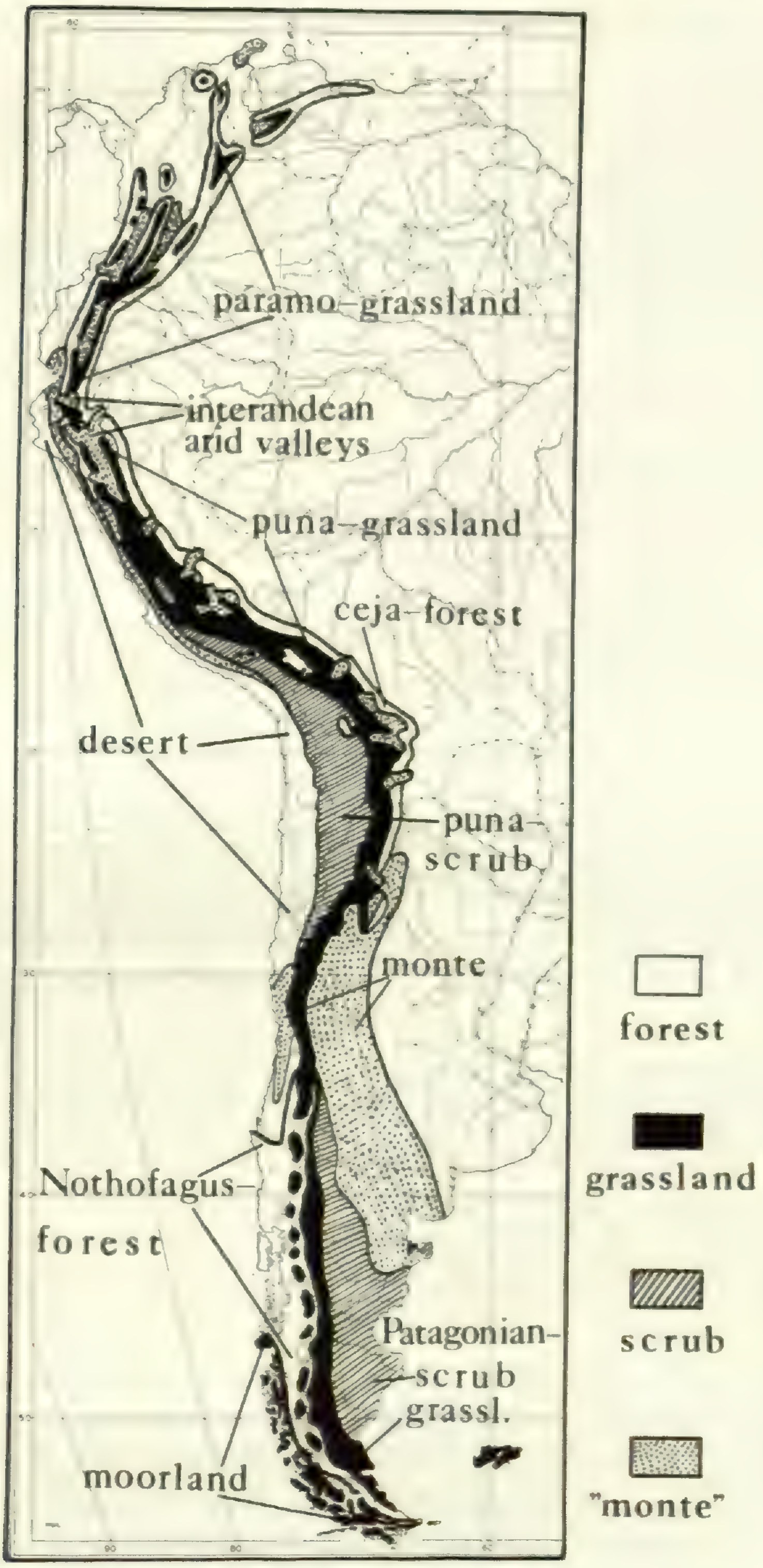


FIG. 4. General vegetation of the Andes showing the major vegetation types.

continent and on Tierra del Fuego and surrounding islands (cf., Skottsberg, 1916; Godley, 1960), where two species are present.

The specific habitats of individual species are discussed in PART II under each species, and are summarized in Table 2.

Physiological Adaptations. Since most (71 per cent) of the species occur in areas with a dry climate (Table 2) and/or high altitudes (with frequent frosts), they have many adaptations to xerophytic conditions. Some of these adaptations are reflected in the time of flowering, type of growth and habit, and seed germination.

Flowering seems to be under the influence of several external factors such as day length and temperature regime. Moreover, it appears that most, if not all, species of *Perezia* sect. *Perezia* do not flower during the first several years of growth. All attempts to stimulate flowering in the greenhouse have failed. In contrast to the South American species, two species of the North American section *(P. thurberi* and *P. microcephala)* grown in the greenhouse flowered abundantly the first year they were sown. These two species are perennials, as are the South American species, but they are weedy, fast growing, and occur at low elevations.

Troll (1959) and Hedberg (1964) have shown that, for tropical high altitude plants, the most important climatic influence is the extreme range in diurnal temperature. In high tropical mountains the daily temperature difference far exceeds the yearly range. As a consequence, plants growing at high altitudes (over 3000 m) in tropical latitudes are adapted to having the soil (and thus the available water) frozen nightly while during the day air temperatures may reach as high as 30° C. Studies have shown (Hadley & Bliss, 1964; Mooney & Billings, 1965) that plants which are adapted to high altitudes suffer from "over respiration" at low altitudes when grown under usual conditions. None of the *Perezia* plants from the tropical montane areas of South America survived for more than one year in the greenhouse in Cambridge, Massachusetts, and all of the plants were stunted, producing few leaves during the one year of growth.

For species growing in the Southern Andes (south of 30° S), the seasonal changes in temperature (rather than the diurnal changes) and day length are probably the primary influences in initiating growth and flowering. In contrast, all of the species brought from the southern part of South America (except *Perezia lactucoides*

subsp. *palustris*, a swamp plant) survived three years in the greenhouse at Cambridge, although none flowered. It is possible that these plants from temperate areas could have been induced to flower under carefully controlled conditions, i.e., in a growth chamber. Since such facilities were not available, and because it would have been a study in itself, this was not attempted.

Seed germination also appears to be different in high and low altitude species. The causes of seed dormancy (or complete failure of germination) of alpine plants are apparently very diverse and little understood (Bliss, 1956; Amen, 1966). Amen (1966), working at sea level with a sample of alpine species, found that over half of his species had less than 50 per cent seed germination. Stratification did not help to increase germination in his samples. However, because of the limited scope of Amen's study, his results cannot necessarily be extended to the majority of high altitude species.

Germination rates proved to be higher when the achenes of *Perezia* were sown on loose soil rather than filter paper, but in both instances they were extremely low. Achenes of 16 species of *Perezia* were sown on loose soil in small pots; of these, seeds of only eight species germinated. Germination in the eight successful lots varied from 1–10 per cent of the total number of achenes sown, except in the case of *P. multiflora* in which 50 per cent of the seeds germinated. Stratification to induce more germination was attempted, but without success. The behavior of *Perezia* seeds thus confirms to some extent the findings of Amen (1966).

Predation. There are two different types of predation on plants of *Perezia*, one directly or indirectly involving man, and the other an insect. Predation by man is due to the destruction of populations and their habitats by farming and grazing of domestic animals. At Checayani, near Azángaro, Perú, where only a few plants of *Perezia* could be found, I have seen plants being eaten by sheep. The few specimens collected were confined to soil too poor to support enough vegetation for extensive sheep grazing, or were near the hacienda where animals were not allowed. Boelcke (1957) has documented for Patagonia that grazing can have an effect on the composition of the vegetation of an area.

Grazing can also affect the habit of a species as shown by Kemp (1937) for *Poa pratensis* and *Trifolium sp.* Selection pressure from grazing animals undoubtedly contributes to the ap-

pressed habit of several altiplano species and for the spiny, cushion plant-like habit of the Patagonian steppe.

Populations of *Perezia* have been destroyed by farming all along the Andes. Seed germination and growth of most species of *Perezia* is so slow that once plants have been plowed under or uprooted, they do not reestablish themselves, recolonize new areas, or "shift" to roadside areas. Specimen data indicate that populations and species are disappearing from vast areas of South America which have come under cultivation. For example, the number of species of *Perezia* recorded 60 years ago from the areas surrounding Santiago, Chile, far exceeds the number of species which can be found there today. In Perú, the type localities (and only known localities) of two taxa (*P. coriacea* and *P. macrocephala* placed here in synonymy with *P. ciliaris* and *P. pungens*) have been completely destroyed by farming.

Only *Perezia multiflora*, one of the few South American species with a high seed yield and quick seed germination, has become a roadside weed. *Perezia multiflora* also has a selective advantage over other species of *Perezia* in that its plants are extremely spiny and therefore not grazed by cattle and sheep.

The other predator upon *Perezia* is actually a parasite. Adult moths of the family *Muridae* (*Lepidoptera*, identified by Dr. Ellis McLeod) oviposit into the immature capitula early in the spring. The larvae hatch in time to feed on the maturing young achenes, pupate late in the summer, over winter in the capitula, and hatch the next spring. The infestation of these larvae is truly amazing—in some populations there is no plant found which does not have one or two larvae in each capitulum.

Both herbarium specimens and field observation indicate that all species of *Perezia* sect. *Perezia*, except perhaps those of the *P. multiflora* group, are parasitized by these moths. Under these circumstances, it is surprising that a sufficient number of achenes ever reach maturity to keep the populations constant. The longevity of plants of *Perezia* is probably a major factor in keeping the species successful. A similar type of infestation also occurs in at least one species of the North American section. All of the capitula of plants of *P. nana* (sect. *Acourtia*) received from Dr. Leslie Gottlieb were infested with moth larvae.

The species of moths involved in the infestations of either section has not been determined. Several pupae were brought

back from South America, but all attempts to have them complete the molt into the imaginal stage were unsuccessful.

Pollination. Only one pollinator was seen visiting capitula of *Perezia*. In Bariloche, Río Negro, Argentina, all species were regularly visited by an unidentified species of large, orange bumble bee *(Hymenoptera)*. Although apparently no nectar is present in florets of species of *Perezia*, all species sampled have a pleasant, sweet odor probably correlated with bee pollination. In direct contrast to the sweet odor of *Perezia*, species of the related genus *Leucheria* Lag. have a musky, unpleasant smell. The most common insects found on species of this genus were flies.

PALYNOLOGY

Comparative palynology, begun by Wodehouse in the early 1900's and continued by Erdtman, has been used frequently by systematists to clarify problems of relationships in various plant taxa. In order to ascertain its usefulness in the *Nassauviinae* and within the genus *Perezia*, both inter- and intrageneric pollen studies were made.

Pollen grains from at least two species of each nassauviinid genus (except the monotypic genera) were acetolized according to the method outlined by Erdtman (1952, 1960), and compared. The results, except for slight differences, were consistent with those of Wodehouse (1929a) who made a similar study with non-acetolized pollen. As he found, pollen shape and exine morphology is useful in grouping genera within the subtribe. An expanded discussion of the palynology of the *Nassauviinae* and its evolutionary implications will be presented in a later paper concerning the relationships of the genera of the subtribe.

In addition to acetolysis, pollen of two or more specimens of each species of *Perezia* sect. *Perezia* was stained with methylene blue, mounted in glycerine jelly, examined, and measured. This technique, rather than acetolysis, was used for several reasons. First, all previous work done on pollen in the *Mutisieae* was based on non-acetolized pollen (Wodehouse, 1929a; Carlquist, 1957). In order to make the observations comparable, it was felt that direct mounts should be tried. Second, staining with methylene blue allowed a simultaneous check for probable viability of the

pollen. Finally, direct mounts are far simpler to prepare than acetolized specimens. As a control, the diameter of acetolized grains was measured for several species and the measurements were compared with those from non-acetolized preparations: the differences in size were negligible.

The staining of the pollen indicates that there is potentially 100 per cent pollen viability in the different species of *Perezia* sect. *Perezia*. All of the pollen grains took up the stain well and showed no deformities in shape. In a few cases, anthers which were too immature were used and the pollen had not fully expanded. The grains from these specimens were not measured and only turgid grains with bulging pores were used in the analysis.

Table 4 gives the number of grains of each species measured, the mean pollen grain diameter, the standard deviation of the mean, and the coefficient of variation. One hundred grains were measured for each species when possible. When adequate material was lacking, fewer grains were used.

As shown in Table 4, there appear to be three loose categories of pollen grain sizes. The smallest grains occur in the *Perezia multiflora* species group. Grains of intermediate size are found in the *P. magellanica* group, larger grains in the *P. pungens*, the *P. coerulescens* and the *P. recurvata* species groups, and the largest in the *P. prenanthoides* group. Although there are no statistically significant differences in the pollen grain diameters between species groups, there is a tendency for the species within a group to have pollen grains of the same relative size.

At present, no explanation can be given for the differences in pollen diameter. A comparison of the data of Table 4 with those of Table 5 shows that the size differences do not appear to be correlated with differences in chromosome numbers. However, few chromosome numbers are known in the genus.

CYTOLOGY

The cytology of the *Mutisieae* has been little studied to date. Chromosome numbers are known for only about 8 per cent of the species in the tribe (ca. 50 of 630). Within the *Mutisieae*, a diploid number of $2n=54$ has been found in species of such unrelated genera as *Chuquiraga* Juss., *Cyclolepis* Gillies ex D. Don, *Plazia* Ruiz & Pav., *Mutisia* L.f., *Trixis* R. Br., *Proustia* Lag., and

TABLE 4. DIAMETERS OF POLLEN GRAINS OF PEREZIA SPECIES

Species of *Perezia*	Number of grains	Mean diameter	Standard deviation of mean	Coefficient of variation
P. multiflora	100	28.8	1.7	5.9
P. squarrosa	100	30.1	1.4	4.7
P. kingii	100	24.4	1.7	7.0
P. prenanthoides	100	41.4	1.9	4.4
P. nutans	100	38.9	2.5	6.4
P. pungens	100	38.5	1.6	4.4
P. sublyrata	100	39.8	1.8	4.6
P. mandonii	50	39.4	1.7	4.2
P. ciliosa	100	35.7	1.8	5.1
P. purpurata	300	42.5	2.5	6.0
P. pilifera	100	35.2	2.1	5.9
P. carthamoides	100	37.4	2.2	6.1
P. viscosa	110	36.7	1.9	5.2
P. lactucoides	50	35.7	1.4	4.0
P. pedicularidifolia	135	35.0	3.6	10.0
P. lyrata	156	36.9	2.7	7.3
P. fonkii	100	35.8	1.5	4.2
P. delicata	50	38.1	2.7	7.1
P. magellanica	100	32.3	4.9	14.9
P. calophylla	100	36.8	1.2	3.4
P. bellidifolia	110	34.8	2.2	6.3
P. megalantha	100	38.9	1.5	3.8
P. coerulescens	300	42.9	2.0	6.0
P. pinnatifida	50	34.9	2.4	6.9
P. pygmaea	100	37.2	1.6	7.2
P. poeppigii	100	39.0	3.0	7.9
P. linearis	100	40.5	2.2	5.5
P. recurvata	270	37.3	2.3	6.0

Perezia sect. *Acourtia*. Diploid counts of $2n=8$, 16, 24 (26), 40 and 48 have been reported in *Pertya* Sch. Bip., *Ainsliaea* DC., *Chaptalia* Vent., *Leucheria* Lag., and *Perezia* sect. *Perezia*. The only number in common between these two groups of genera is $2n=26$ now recorded from *Mutisia*, *Pertya* and (perhaps) *Perezia* sect. *Perezia*.

The karyology of species of the *Mutisieae* is even more poorly known than the chromosome numbers. However, a survey of published chromosome photographs and drawings, shows two things: the karyotypes of species with numbers of $2n=8$, 16, 24, 40, 48

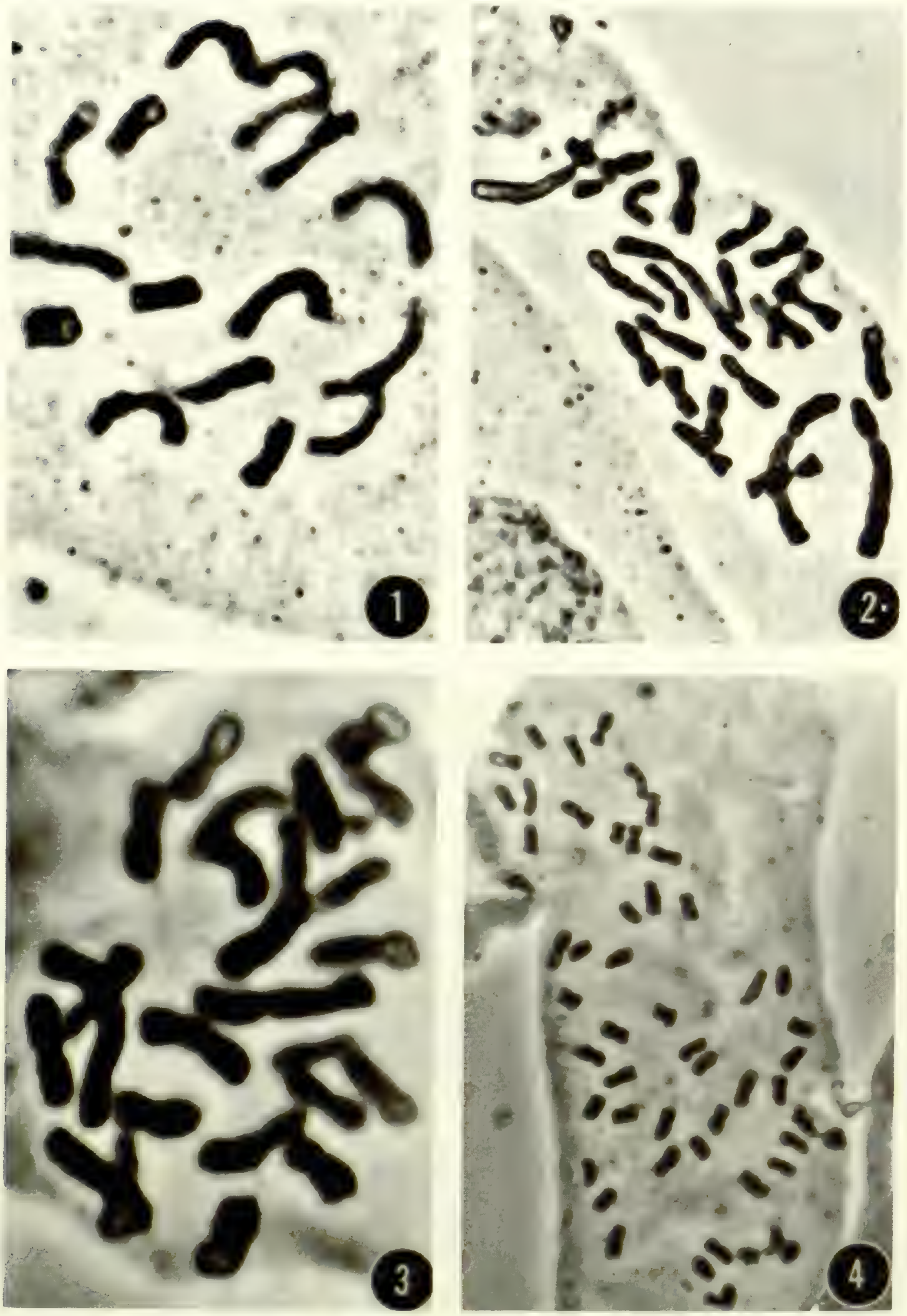


FIG. 5. Chromosomes of selected species of *Perezia*. FIG. 5–1, *P. multiflora* (2n=16); 5–2, *P. calophylla* (2n=24); 5–3, *P. ciliosa* (2n=24). FIG. 5–1 to 5–3 are all from species of *Perezia* sect. *Perezia* and show a karyotype composed of a mixture of long and short chromosomes. FIG. 5–4, *P. thurberii* of sect. *Acourtia* shows a compliment of 2n=54, small, equal sized chromosomes. All photographs are taken from root tip cells stained in basic Feulgen.

(52) show a mixture of long and short chromosomes (cf., Fig. 5–1 to 5–3) while those species with a complement of $2n=54$ seem to have very small chromosomes of more or less equal size (Fig. 5–4).

Table 5 lists the chromosome numbers now known in *Perezia;* five of these counts are reported here for the first time, and two previous counts are confirmed. Figures 5–1 to 5–3 show mitotic chromosomes (from root tips fixed in 8-oxyquinoline and stained in Feulgen) of selected species of *Perezia* sect. *Perezia* and Fig. 5–4 contrasts the karyotype of a species of sect. *Acourtia*.

TABLE 5. CHROMOSOME NUMBERS IN PEREZIA

TAXON	*n*	2*n*	REFERENCES
Perezia sect. *Perezia*			
P. multiflora		16	Diers, 1961; Vuilleumier. Sneider, unpub.
P. squarrosa subsp. *cubaetensis*	4		Coleman, 1968.
P. pungens		24	Heiser, 1963.
P. ciliaris		24	Vuilleumier.
P. carduncelloides	12		Sneider, unpub.
P. ciliosa		24	Vuilleumier.
P. calophylla		24	Vuilleumier.
P. coerulescens		24	Diers, 1961; Vuilleumier.
P. recurvata		24 or (26)	Vuilleumier.
Perezia sect. *Acourtia*			
P. microcephala A. Gray		54	Raven, *in litt.*
P. thuberii A. Gray		54	Vuilleumier.

The chromosome number and karotype for at least one species of every group of *Perezia* sect. *Perezia* (except the *P. prenanthoides* group) is now known. The counts indicate that four is the basal number in the South American section because gains in chromosome number (by polyploidy or aneuploidy) are much more common in the Angiosperms than decreases (Stebbins, 1950), especially when the equivalent of an entire complement is involved and intermediate stages are not found. In other words, it is much more probable that $n=4$ (now known in *P. squarrosa* subsp. *cubaetensis*) was ancestral, and that $n=8$, and $n=12$ (13) were derived rather than the reverse.

However, more counts are necessary to completely clarify the picture. At this time it is particularly difficult to relate the numbers

and karyology of the two sections of *Perezia,* but future counts of the species of this and related genera should add to our understanding of evolution in the *Mutisieae.*

CHEMOTAXONOMY

Chemical taxonomy is a comparatively recent method employed by plant systematists that clarifies problems of relationship (McClure and Alston, 1966) and hybridization (Alston and Turner, 1963 a,b). The majority of chemical taxonomic studies have been made using a class of compounds known as the flavonoids, but systematic work has also been done using other groups of chemicals—most recently, enzymes. Comparative enzymology, as stated by Alston (1967), may be one of the most elucidating approaches of any chemotaxonomical work. Enzymes were not used in early studies because, until the last few years, it was more difficult to work with them than with other classes of chemicals.

Because of the relative ease of dealing with flavonoids and their previous widespread use in the taxonomy of several plant families, I decided to make a preliminary survey of the flavonoid chemistry in *Perezia* sect. *Perezia.* This study was not intended as a detailed analysis, but merely an exploration of distribution patterns of flavonoids in the section to see whether more extensive chromatography was indicated. This initial survey was made for two purposes: possibly to solve existing taxonomic problems in the genus *Perezia;* and, to explore chemotaxonomy and its application in the systematics of the *Nassauviinae.*

Methods. The extraction and two dimensional descending chromatography techniques of Alston and Turner (1963) were used with butanol:acetic acid:distilled water (3:1:1 v/v) as the first solvent, for 24 hours; and acetic acid:distilled water (15:85 v/v) as the second solvent, for 4–6 hours. The chromatographs were inspected under daylight, longwave ultraviolet light, and under both conditions with ammonia vapor. Voucher specimens have been deposited in the Gray Herbarium.

Discussion. Before discussing the results obtained from the chromatography of *Perezia* leaf extracts, it must be pointed out that only a few individuals of a few representative species were analyzed chromatographically (in some cases only one individual). Several individuals from numerous populations of each

FIG. 6. Localities of specimens of *Perezia* used in paper chromatography analysis. Names with dots are actual localities, names without dots are provinces or departments.

species should be chromatographed, and all species should be sampled for a truly accurate comparison. It should also be emphasized that none of the spots were eluted and purified to give chemicals that could be identified. In some cases the groups of flavonoids could be determined for certain spots, in others they could not. In general, only the spot patterns and characteristic reactions of the spots were used, and as such were considered as a morphological character.

Figures 7 to 13 give the patterns of selected chromatograms and Table 6 gives the different spot color reactions. Unless it was quite certain that the spots in different chromatograms represented the same chemical they were assigned different numbers. When the same number is used for a spot in more than one chromatogram, the compound at that spot is presumed to be the same in both cases. Figure 6 gives the localities of the specimens used in the chromatographic analysis.

A superficial glance at the chromatograms reveals considerable variation in the spot patterns within a species—even those which are constant in gross morphology. (Cf., Fig. 7–1 with 7–4; 7–2 with 7–3; 12–3 with 12–4; and 10–3 with 10–4.) There is, however, a greater amount of variation in the chromatographic patterns of the species that are more variable in gross morphology than in those that are less variable (see PART II, Taxonomy, for discussions of morphological variation). A pertinent example of this contrast is between *Perezia purpurata*, composed of several isolated series of populations, each morphologically distinctive (Fig. 23), and *P. multiflora*, a wide ranging species with relatively little morphological variation (Fig. 8–1 and 8–4 compared with 10–3 and 10–4).

Similarly, in a species such as *Perezia recurvata* with several polymorphic phenotypes, there is considerable intrapopulation variation in chromatography patterns (Fig. 11–1 to 11–4). Also, the spot patterns are more similar between species of the same species group than between those of different groups. In other words, a taxonomy erected on the basis of only the chromatograms would lead to a grouping of taxa that agrees roughly with that based on morphology (within the limits of the material tested).

A few spots appeared consistently throughout the tests. Two spots, 1 and 2, were useful as indicators on the different chroma-

FIG. 7. Chromatograms of *Perezia nutans* and *P. prenanthoides*, the only two members of the *P. prenanthoides* species group.

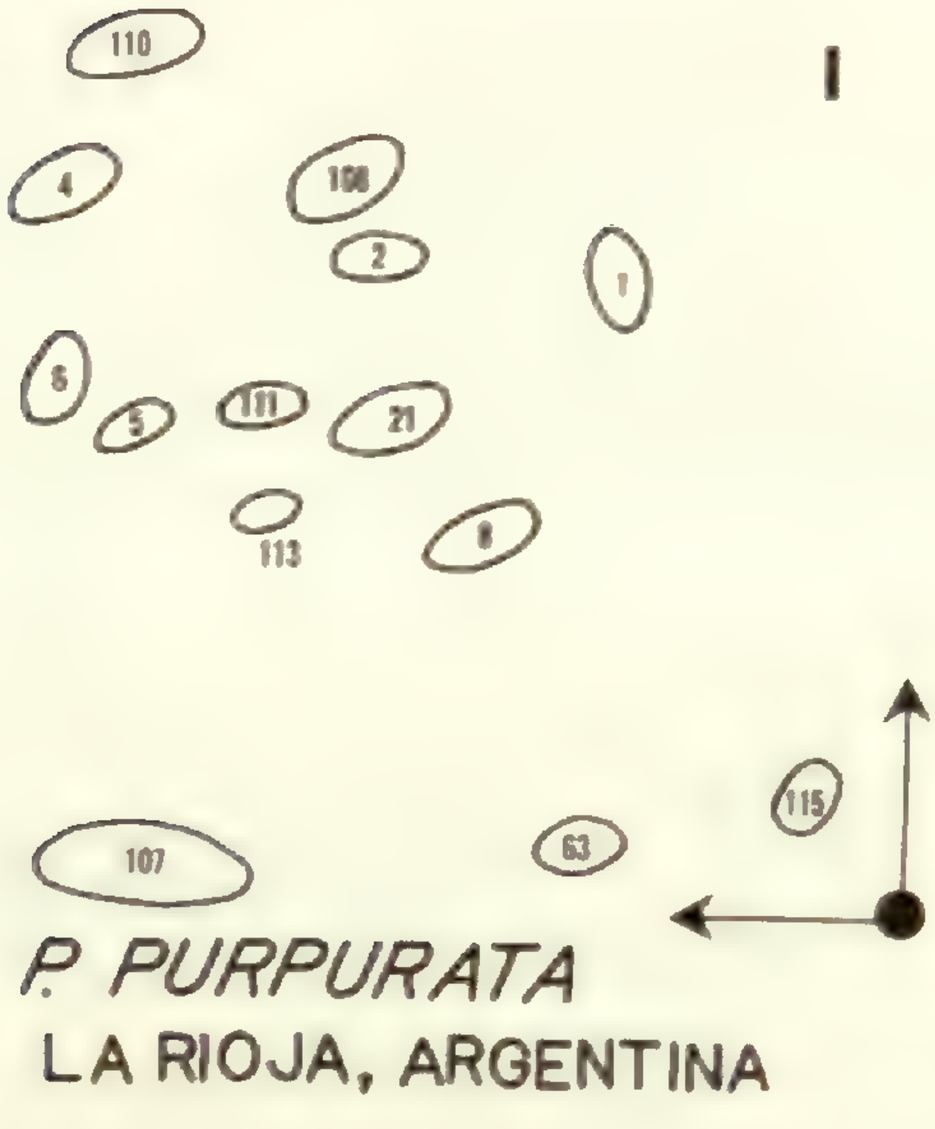
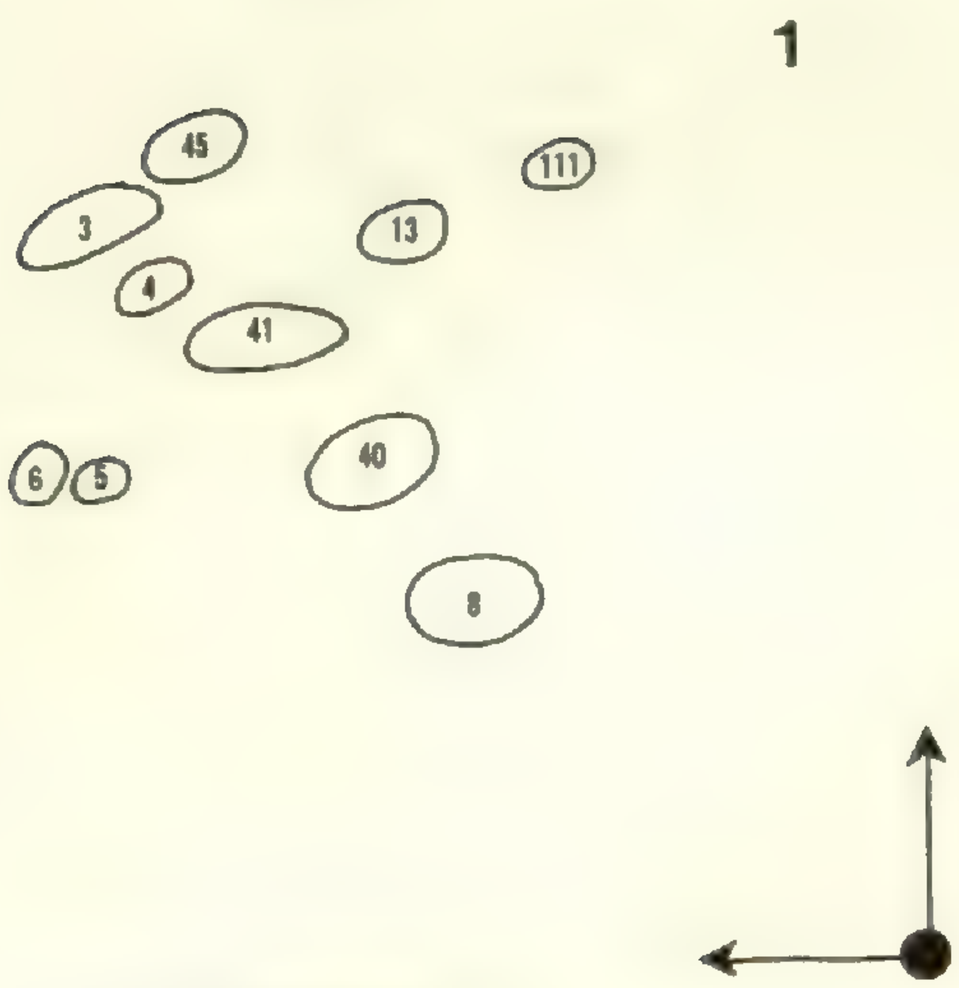
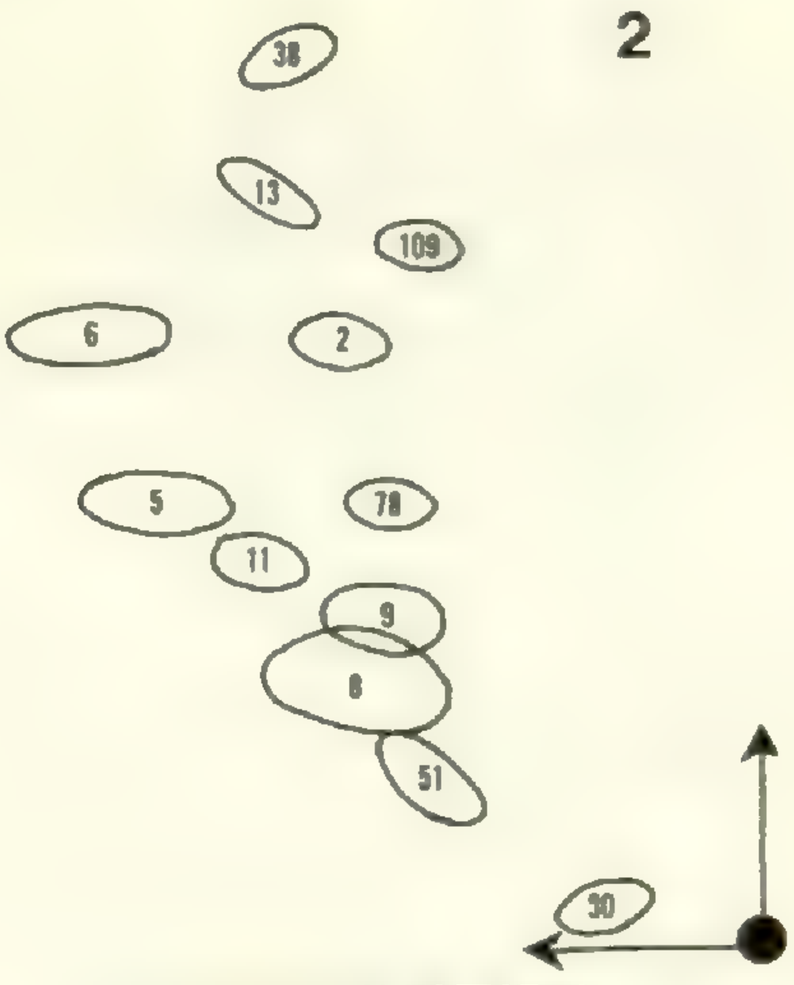


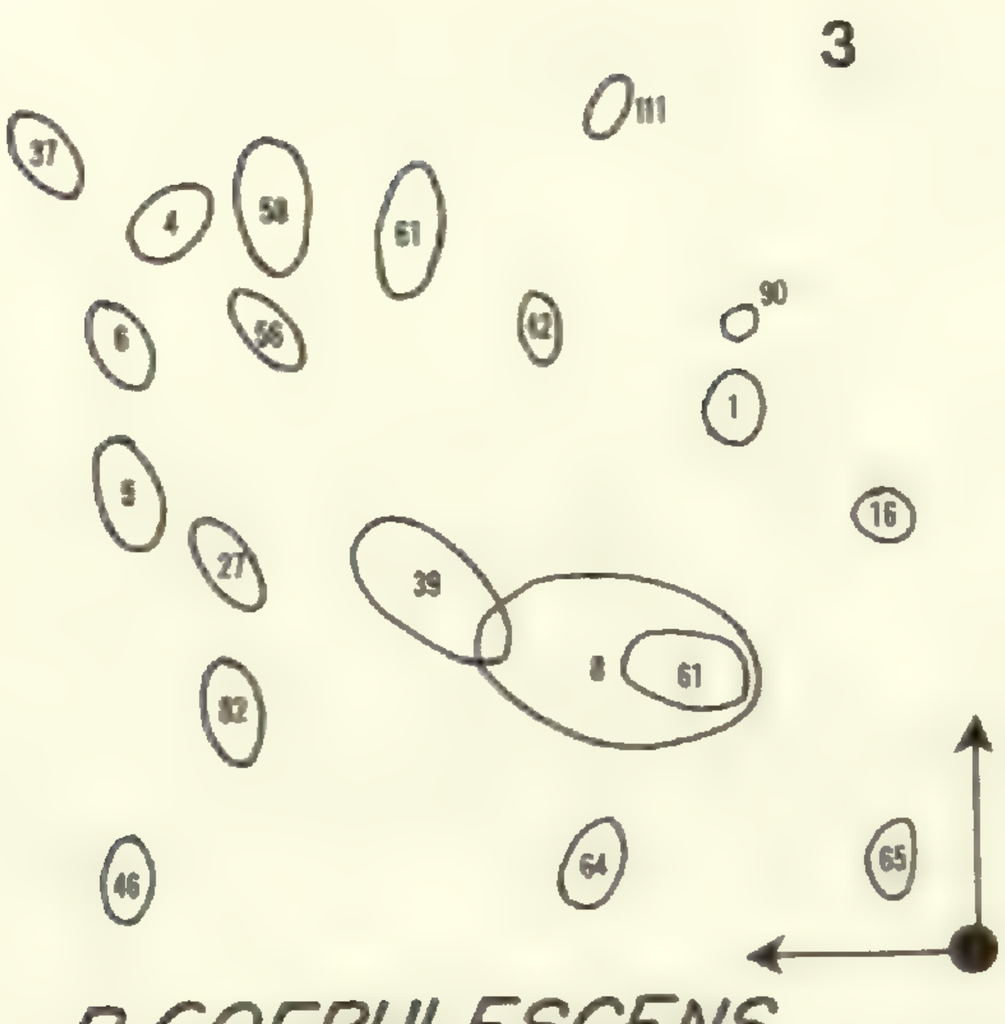
FIG. 8. Chromatograms of four disjunct populations of *Perezia purpurata* (see FIG. 23), a member of the *P. pungens* species group.



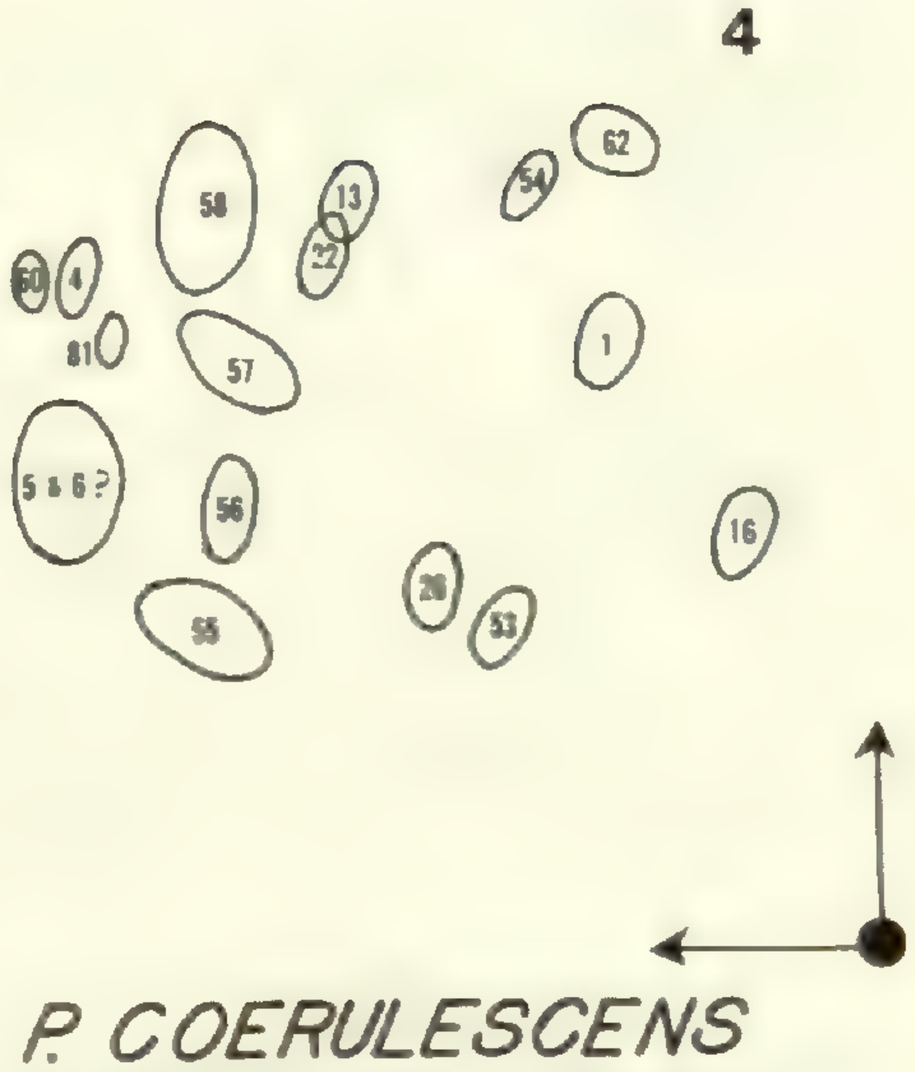
P. PYGMAEA
CASAPALCA, JUNÍN, PERÚ



P. PINNATIFIDA
LIMA, PERÚ

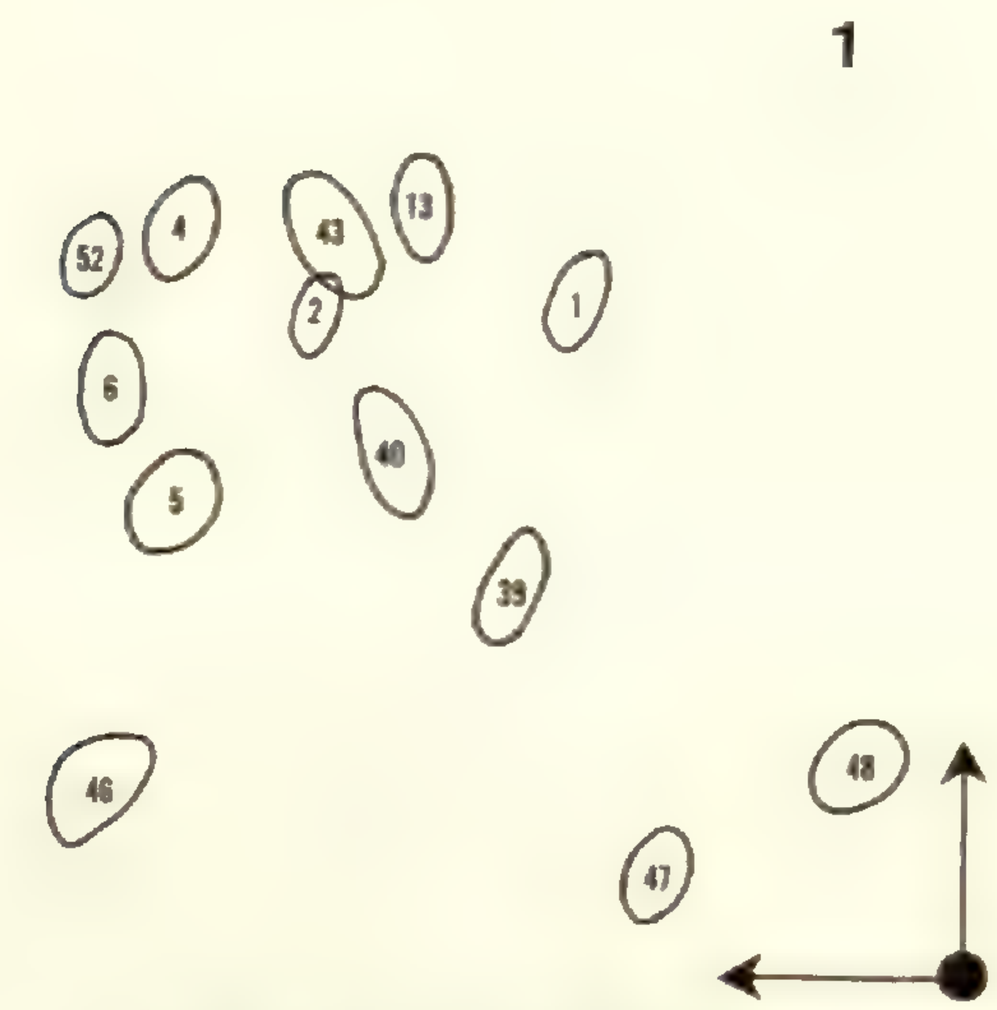


P. COERULESCENS
LA PAZ, BOLIVIA

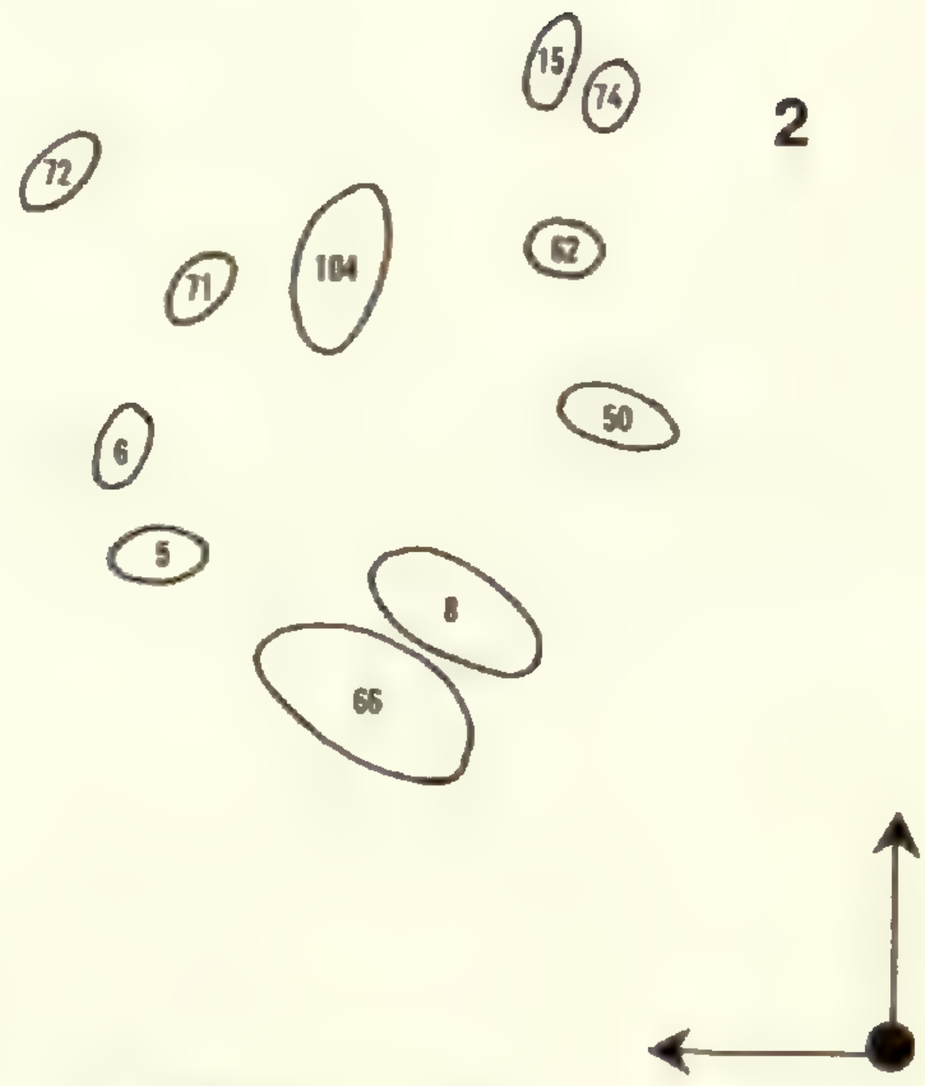


P. COERULESCENS
COCHABAMBA, BOLIVIA

FIG. 9. Chromatograms of the three members of the *Perezia coerulescens* group: *P. pygmaea, P. pinnatifida,* and *P. coerulescens.*

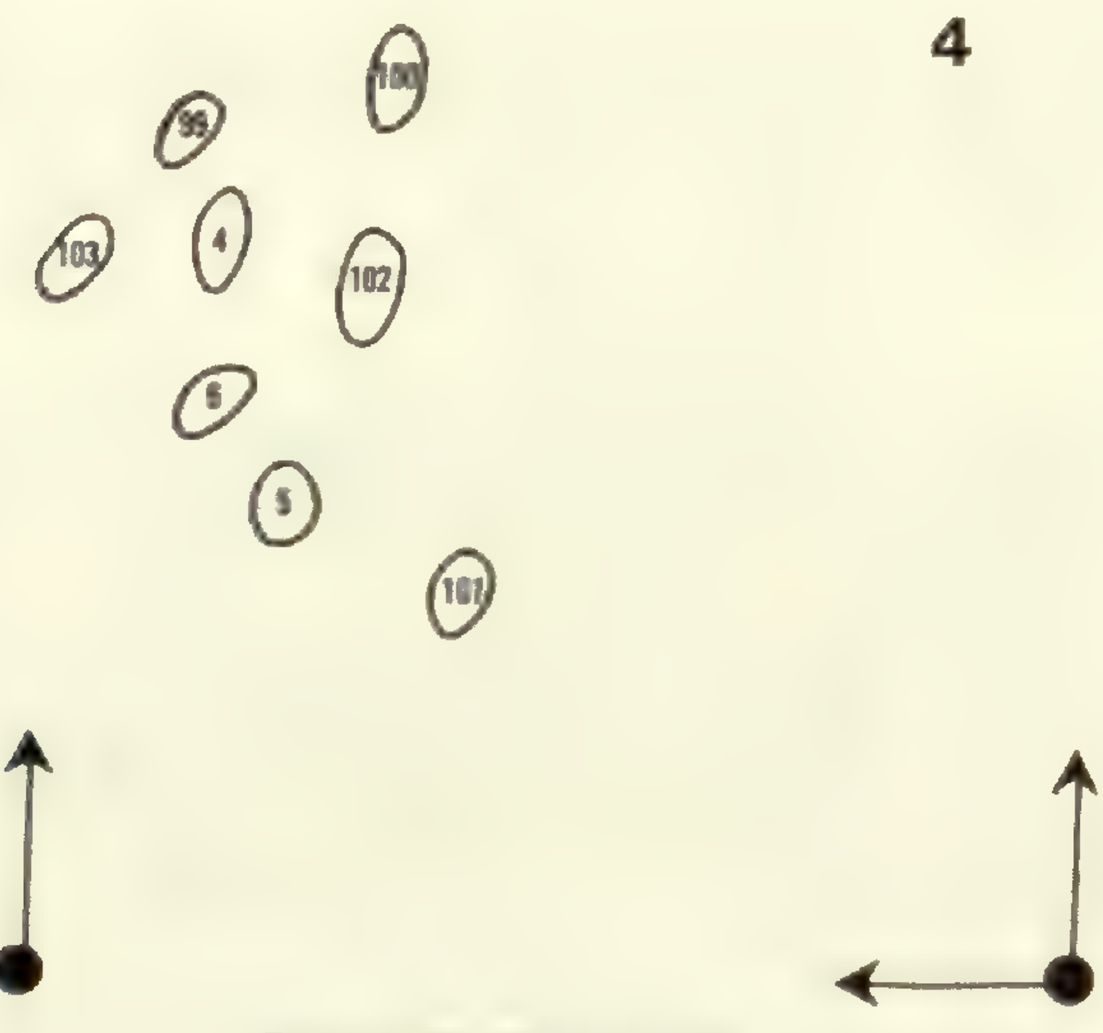


P. COERULESCENS
SIERRA DE CALCHAQUIES, ARGENTINA



P. PYGMAEA
JUJUY, ARGENTINA

P. MULTIFLORA
MT. PICHINCHA, ECUADOR

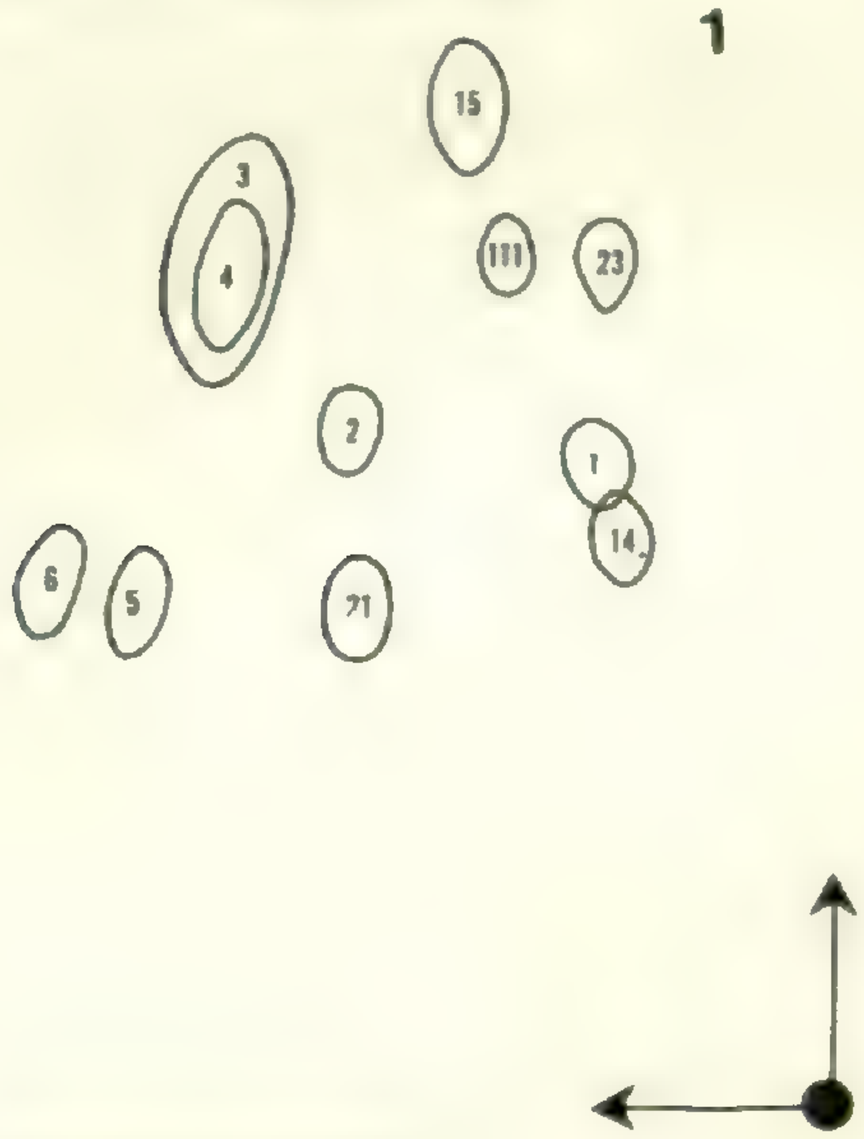


P. MULTIFLORA
JUJUY, ARGENTINA

FIG. 10. Chromatograms of *Perezia coerulescens* and *P. pygmaea*, both members of the *P. coerulescens* group, and *P. multiflora*, one of the three species in the *P. multiflora* species group.

"TRICEPS" PHENOTYPE

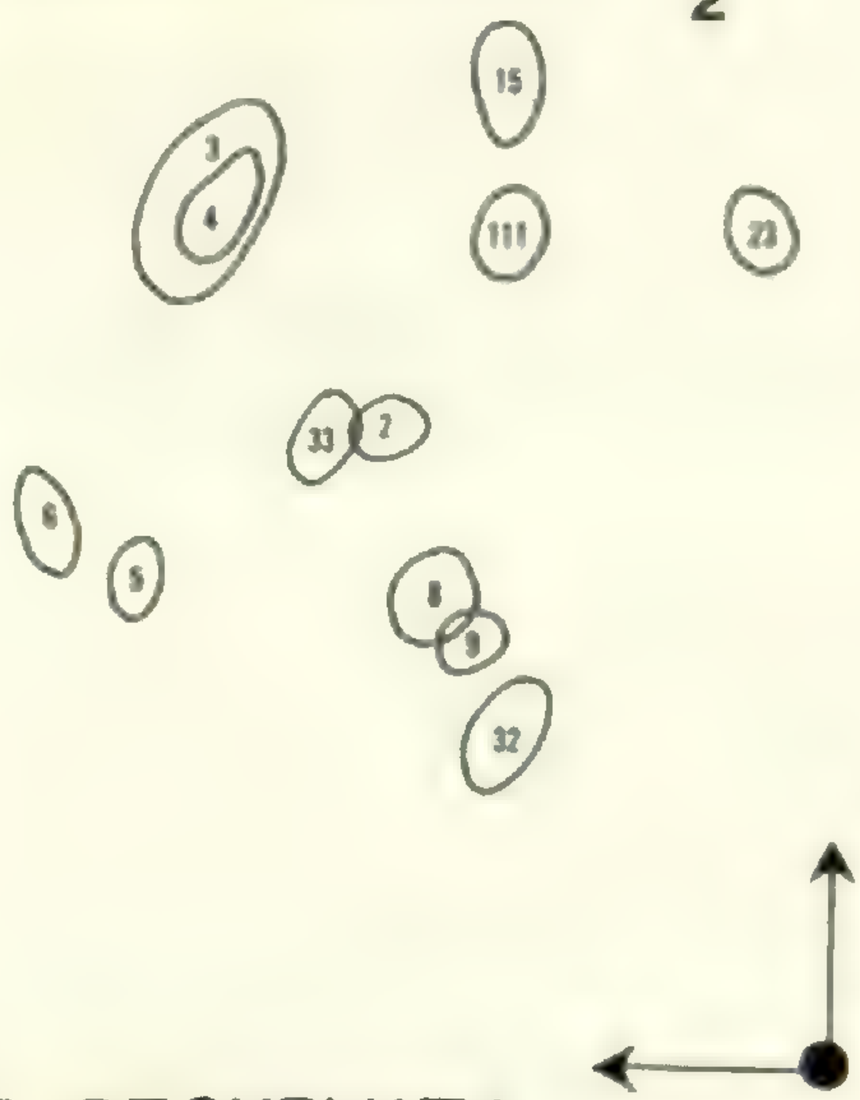
1



P. RECURVATA
PILCANIYEU, RÍO NEGRO,
ARGENTINA

"BECKEII" PHENOTYPE

2



P. RECURVATA
PILCANIYEU, RÍO NEGRO,
ARGENTINA

3

"BECKEII" PHENOTYPE

P. RECURVATA
PUERTO DESEADO
SANTA CRUZ, ARGENTINA

4

"BECKEII" PHENOTYPE

P. RECURVATA
SAN JULIÁN, SANTA CRUZ,
ARGENTINA

FIG. 11. Chromatograms of various phenotypes of *Perezia recurvata* (see FIG. 27 and 28), the most specialized members of the *P. recurvata* species group.

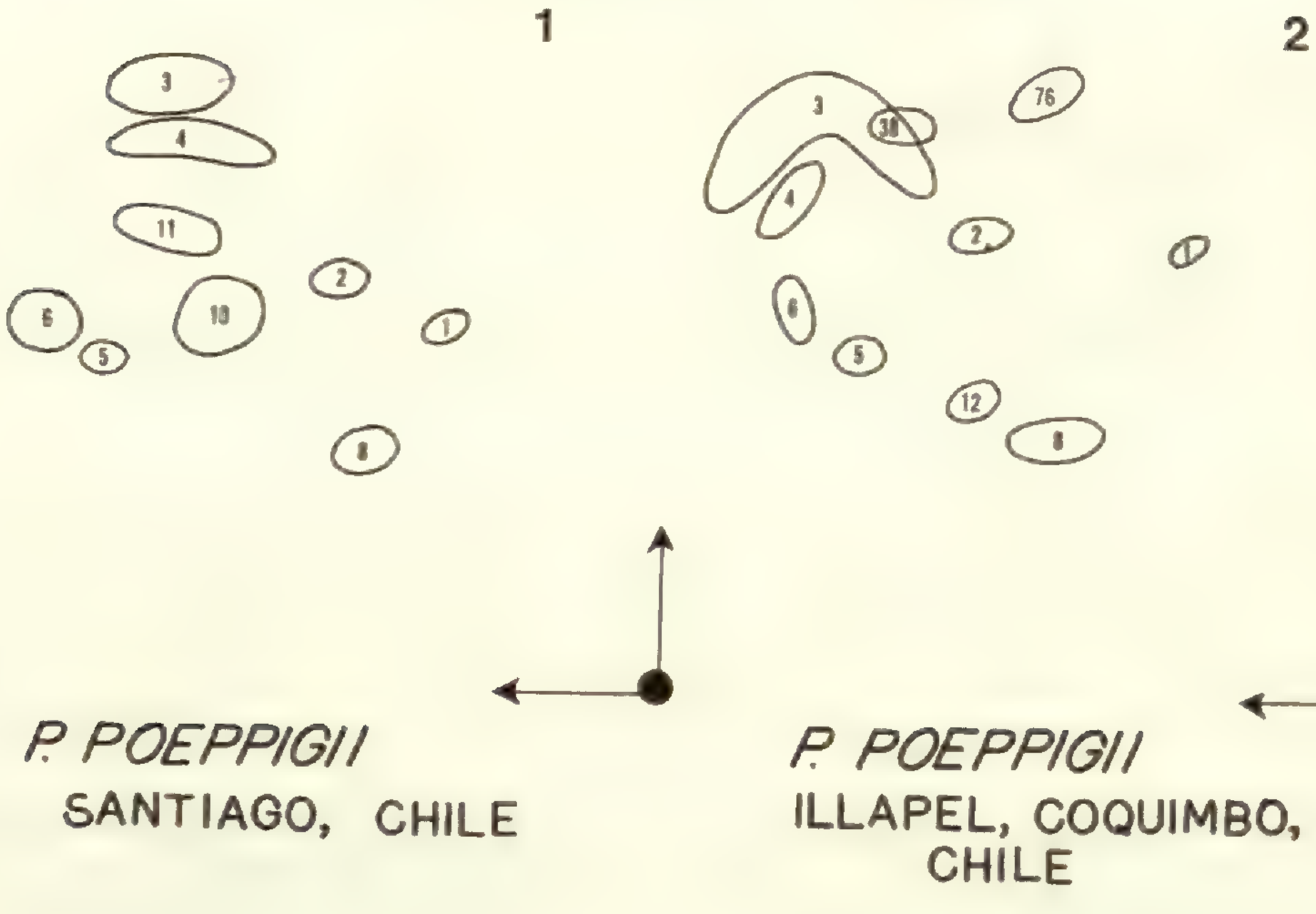


FIG. 12. Chromatograms of two populations of *Perezia poeppigii*, the least specialized member of the *P. recurvata* species group and *P. carthamoides*, the member of the *P. pungens* group to which *P. poeppigii* appears most closely related.

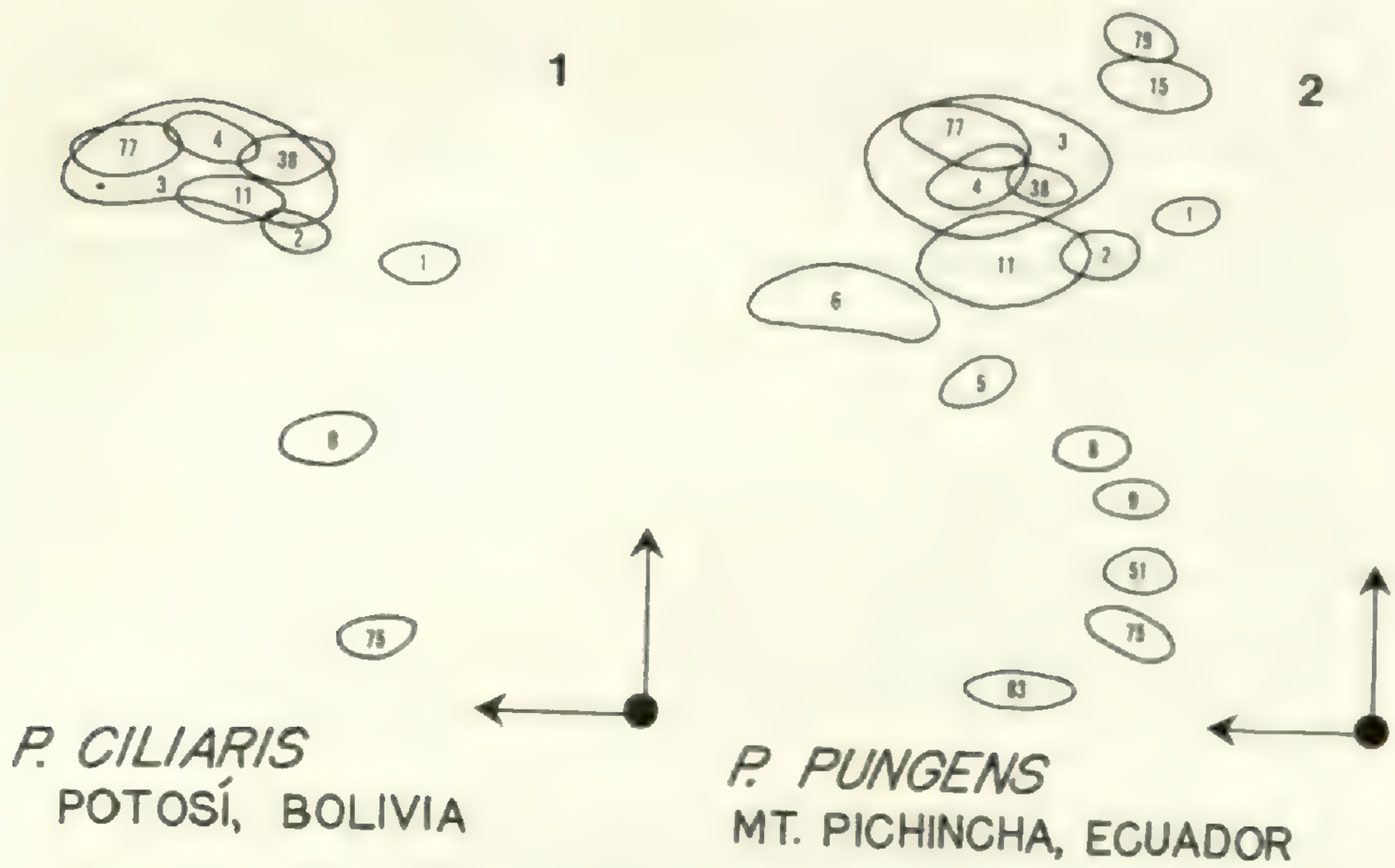


FIG. 13. Chromatograms of *Perezia pungens*, its nearest relative, *P. ciliaris*, and another species of the *P. pungens* group, *P. ciliosa*. A chromatogram of *P. pilifera*, a very unique species in the genus, is added for comparison.

tograms. Their pink fluorescence in ultraviolet light and their relative positions made them readily identifiable. One or both of these spots were present in most specimens examined, except those of *Perezia multiflora*, *P. nutans*, and *P. prenanthoides*. Three other spots, designated as 4, 5, 6 were also present in most of the chromatograms.

Each of these initial observations appears to be consistent with the findings of chromatographic studies of other plant taxa. Intraspecific and intrapopulation variation of flavonoid compounds has been little studied, but it has recently received more attention from those working in chemotaxonomy. Brehm (1966) reviewed the literature on variation of plant compounds and came to the conclusion that future research would show that the same type of variation is present in the secondary chemicals of a plant species as in any morphological character. Brehm (1966) also cited the work of Horn (unpublished Ph.D. thesis, University of Texas) whose research showed that a large amount of intrapopulation variation was present in *Baptisia nuttalliana (Leguminosae)*. Some flavonoids were always present and others were, he felt, randomly distributed in the population.

Alston (1967), however, postulated that the more variable compounds which Horn found were not randomly distributed, but rather followed microclinal geographical gradients of some kind. Flavonoid compounds would, according to Alston, presumably be under the same influences as other phenotypic characters —different selection pressures in geographically separated parts of the range. Alston illustrated (1967) the chromatograms of two geographically separated populations of *Baptisia leucantha* and four populations of *Hymenoxys scaposa (Compositae)*. The variation present in these chromatograms is as great as, or greater than, any interpopulation variation of flavonoids I found in *Perezia*.

Problems Attacked in Perezia. Because material available for analysis was limited, attention was focused on problems which could be profitably attacked by chromatography. But first chromatographs were run on different specimens of several species to see whether there were distinct patterns present in different species of *Perezia*, and to determine whether these patterns appeared to be species specific. Preliminary chromatograms indicated that there were more similarities in the patterns of

flavonoid and phenolic spots within a species than between different species. (See, for example, Fig. 7–2 and 7–3; 12–3 and 12–4; 10–3 and 10–4.) Therefore, it was assumed that chromatography would indicate affinities between species. With this as a working hypothesis, the following specific questions were investigated:

1. Would an analysis of flavonoid compounds of the two closely related species *Perezia prenanthoides* and *P. nutans* allow them to be separated on the basis of their spot patterns and reactions? To what species, or groups, do the two members of this apparently isolated species group seem to be related on the basis of their chromatograms?
2. Would the isolated populations included in *Perezia purpurata* show similarities in flavonoid compounds? Are the chromatograms of these populations as similar to each other as those of separate populations of other species, confirming or countervailing the decision to place them in one large variable species?
3. Would chromatographic data be of use in solving the taxonomy of the *Perezia coerulescens* complex? On the basis of chemical analysis, to what species group would the *P. coerulescens* complex appear to be related?
4. Would chromatographic evidence indicate that all forms of *Perezia recurvata* were merely phenotypes of one species or sibling species? To what other species and species group would *P. recurvata* and its ally *P. poeppigii* appear to be related?

RESULTS

1. The two species, *Perezia prenanthoides* and *P. nutans*, showed very similar chromatographic patterns (Fig. 7–1 to 7–4) with the spot patterns and reactions strikingly paralleling the strong morphological similarity between the two species. The chromatograms of the two species were so alike that it would be impossible to separate them on the basis of spot patterns and reactions alone. However, an analysis of the actual compounds involved might show species specific differences.

Superficially, the spot patterns of the two species of the *Perezia prenanthoides* group were like those of *P. multiflora* (compare Fig. 7–1 to 7–4 with 10–3 and 10–4). However, it must be noted that although there was a resemblance in the simplicity of their spot patterns, the actual positions of the spots (R_f values), and the color reactions were very different in the two cases. Morphologically, species of the *P. prenanthoides* alliance are quite distinct from those of the *P. multiflora* group. Thus the similarities of the spot patterns are considered to be the result of convergence, rather than a reflection of close affinity.

A comparison of the chromatograms of the two species of the *Perezia prenanthoides* group with the other species tested did not show any similarities indicating affinities of this group to the other species in the section.

2. Interesting chromatographic data were obtained from an analysis of the different populations of *Perezia purpurata*. The overall similarity, in both spot position and characteristics on the chromatograms from specimens collected in different populations (Fig. 8), indicates a close affinity of the populations. Moreover, the pattern of the specimens of *P. purpurata* from Atacama, Chile was most similar to the pattern of the specimens from La Rioja, Argentina. Of all of the major populations of this species, these two are the most similar morphologically (Fig. 8–1 and 8–2).

Only one poorly dried specimen of *Perezia purpurata* from the Sierra de Calchaquíes was available for study, but the incomplete chromatogram obtained from this specimen (Fig. 8–3) was definitely similar to that of the specimens from Jujuy, Argentina (Fig. 8–4). As discussed under the taxonomic treatment of *P. purpurata,* there is an indication of gene flow between the Sierra de Calchaquíes and the Jujuy populations.

3. The limited analysis of representatives of the *Perezia coerulescens* complex did not clarify any of the important taxonomic problems encountered in this group, but did indicate that it is an extremely variable assemblage. Although the chromatograms of the three species of this group are slightly similar (Fig. 9–1 to 10–2), there is an almost hopeless diversity present (perhaps also indicating that the treatment suggested here is not the most natural one possible).

In this case, the chemotaxonomical data added little to supplement or counter other evidence. Yet, one suggestion emerges from the flavonoid patterns—the *Perezia coerulescens* complex appears to be related to the *P. pungens* group through *P. purpurata,* rather than to *P. carthamoides* or *P. poeppigii* as might be assumed from gross morphology alone (Fig. 9–1 to 10–2 compared with 8–3 and 8–4 vs. 12–3 and 12–4).

4. The analysis of the chromatography of *Perezia recurvata,* another confusing species, was almost the antithesis of that of the *P. coerulescens* complex. Instead of an array of different patterns, there was a similarity in chromatograms of different phenotypes from the same population (Fig. 11–1 and 11–2), the same phenotype from closely situated populations (Fig. 11–3 and 11–4), and from widely separated populations (Fig. 11–2 and 11–3). The chromatograms of the same phenotype, whether from the same or different populations, were no more similar than those of different phenotypes. The similarity of all of the patterns adds evidence to the biological interpretation presented here (PART II), namely, that one species, with areas of secondary contact between formerly isolated populations, is involved.

Although the *Perezia recurvata* and the *P. coerulescens* species groups are, to some extent, ecological counterparts in the Patagonian and central puna steppes, respectively, their histories have been different, and have created totally divergent biological situations. Moreover, the two complexes appear completely unrelated (compare Fig. 9 and Fig. 11 which show the contrast in flavonoid chemistry in species of these two groups).

The patterns of the specimens of *Perezia recurvata and P. poeppigii* (Fig. 11, 12–1 and 12–2) indicate that these species have chemical affinities with *P. carthamoides* (Fig. 12–3 and 12–4), a species which is a member of the *P. pungens* species group. On the basis of their flavonoid chemistry, the relationships of these two unrelated groups to different segments of the *P. pungens* group reemphasizes the conviction that *P. pungens* and its allies are the modern remnants of the plexus from which several major lineages diverged. One line apparently led through *P. poeppigii* to *P. recurvata,* and another to the still actively speciating *P. coerulescens* complex.

Unfortunately, not enough material was available to study the species of the *Perezia magellanica* assemblage or many members of the *P. pungens* alliance. One specimen of *P. pungens* and its closest relative, *P. ciliaris,* were run (Fig. 13–1 and 13–2) to give at least a partial comparison with the other species sampled.

One specimen of *Perezia pilifera* (Fig. 13–3) was chromatographed to see whether the flavonoid patterns of this unique species would give any clues to its affinities. Morphologically and anatomically *P. pilifera* is very divergent from the other members of the section. The chromatography

pattern proved to be just as distinct as the morphology. The kinds of spot reactions and a part of the spot pattern are more similar to those of *P. purpurata* and *P. pungens* than any other species examined, suggesting an affinity with these two species.

Conclusions. Although no specific problems encountered in a taxonomic study of *Perezia* sect. *Perezia* were solved, a chemotaxonomical survey of several of its members did provide some useful information. The following are among the conclusions arrived at:

1. An array of flavonoids and phenols is present in the basal leaves of flowering specimens of *Perezia* sect. *Perezia* and the kinds and the presence or absence of these compounds vary in different individuals, populations, and species of the section.

2. Despite the variation present, the hypothesis of Brehm (1966) that "even in sexually outcrossing individuals, similarity of patterns (chromatography) should reflect relationships" appears to hold true in *Perezia*. It seems that there is the most similarity in chromatographic patterns between individuals of the same species, less between species of the same species group, and the least between relatively unrelated species.

3. Within the South American species of *Perezia*, chromatographic analysis of flavonoids and phenols indicated that *Perezia purpurata* and *P. recurvata*, although morphologically variable were internally uniform in their secondary chemical compounds. In contrast, the *P. coerulescens* complex displayed an array of dissimilar patterns as varied as the morphology of the different populations involved in the assemblage.

Several species of the *Perezia pungens* species group showed chromatographic patterns similar to members of different species groups. This strengthens a hypothesis, based on morphology, that *P. pungens* and its allies occupy a central position in the section. One evolutionary line from this central complex includes *P. purpurata* and the *P. coerulescens* group. Another appears to lead from *P. carthamoides* to *P. poeppigii*, *P. linearis* and *P. recurvata*. On the basis of flavonoid chemistry, *Perezia pilifera* appears isolated within the section but shows some similarities to the *P. purpurata–P. coerulescens* lineage.

The *Perezia prenanthoides* species and the *P. multiflora* species groups are both tightly knit assemblages, each of which is an isolated unit in section *Perezia*.

4. There is an indication that future chromatographic analysis

TABLE 6. COLOR REACTIONS OF SPOTS ON PEREZIA CHROMATOGRAPHS[1]

Spot number	*Long wave UV*	*UV + NH_3 vapor*	*Daylight + NH_3 vapor*
1	Br, Pk	O–P	–
2	Pk	–	–
3	P	Y	Y
4	Bl	–	–
5	P	–	–
6	Bl	–	–
7	P	Y	Y
8	P	Br	Y
9	–	–	Y
10	P	Y	Y
11	P	–	–
12	P	–	–
13	Bl	Y	Y
14	–	–	Y
15	–	Y	Y
16	–	Pk	Y
17	Bl	–	–
18	Bl	–	–
19	Bl	Y	–
20	P	–	–
21	Wh	–	–
22	Bl	–	–
23	Bl	–	–
24	P	Y	Y
25	Bl	–	–
26	Br	Y	–
27	Bl	Y	–
28	Bl	Y	Y
29	–	–	Y
30	P	Y	Y
31	Bl	Y	Y
32	P	–	–
33	–	–	Y
34	Bl	–	–
35	Bl	–	–
36	–	–	Y
37	Bl	–	–
38	Wh	–	–
39	P	–	–
40	P	–	–
41	P	–	–
42	–	Bl	Y
43	P	–	–
44	P	Y	Y
45	Bl	–	–
46	P	–	Y
47	–	Pk	–
48	–	Pk	–
49	–	–	Y
50	Wh	–	–
51	–	Y	–
52	Bl	–	–
53	P	–	–
54	Bl	Y	Y
55	Wh	–	–
56	–	Y	–
57	–	Wh	–
58	Bl	Y	Y
59	P	Br	Y
60	P	–	–
61	P	–	–
62	Wh	–	–
63	–	Br	Y
64	–	Br	Y
65	Bl	–	–
66	Bl	Y	Y
67	–	Br	Y
68	–	Br	Y
69	Bl	–	–
70	–	Br	Y
71	–	Y	–
72	–	Bl	–
73	Bl	Y	Y
74	Pk	–	–
75	–	Pk	–
76	Bl	Y	Y
77	Pk	–	–
78	–	Br	Y
79	Br	–	–
80	P	P	Y
81	Bl	–	–
82	Bl	Bl	Y
83	Bl	Y	Y
84	Bl	Y	Y
85	Bl	Wh	Y
86	Bl	–	Y
87	Bl	Wh–Pk	Y
88	Bl	–	–

[1] The chromatograms from which these spots were taken are presented in Fig. 7 to 13. The following symbols are used to indicate the following colors: Pk = pink Bl = blue Wh = white Br = brown P = purple Y = yellow O = orange

TABLE 6. *(cont'd)*

Spot number	*Long wave UV*	*UV + NH_3 vapor*	*Daylight + NH_3 vapor*
89	Bl	–	–
90	P	P	–
91	Bl	–	–
92	Bl	–	–
93	Bl	–	Y
94	Pk	–	–
95	Bl	–	–
96	Bl	Bl	–
97	Bl	Y	Y
98	P	P	–
99	Bl	–	–
100	P	Y	Y
101	Pk	Y	Y
102	Bl	–	–
103	Bl	Bl	–
104	Bl	Y	Y
105	Pk	Y	Y
106	Pk	–	–
107	–	Pk–O	Y
108	Bl	–	Y
109	–	Br	Y
110	Bl	Y	Y
111	Bl	–	–
112	–	Br–Y	Br–Y
113	Pk	–	–
114	–	Br	Y
115	Y	–	–
116	Bl	–	–
117	P	Y	Y
118	Pk	–	Y
119	Pk	Y	–
120	–	Br	Y
121	Bl	Bl	–
122	Bl	Pk	Pk
123	Bl	–	–
124	Bl	Y	Y
125	Bl	–	–
126	Bl	–	–
127	Bl	Pk	Pk
128	Bl	–	–
130=6	Bl	–	–
131	Bl	–	–
132	Bl	Y	Y

would be useful in clarifying problems found in confusing species complexes, and in hybrid situations. Further study should also show whether changes or variations in flavonoid compounds in different individuals follow geographical clines (as suggested by Alston, 1967) or whether there are random fluctuations in certain chemicals (Horn *in* Brehm, 1966).

NUMERICAL TAXONOMY

Numerical taxonomy is a method, used in systematics, which has received considerable attention in the last ten years. However, it should be noted that numerical taxonomy, unlike classical or chemotaxonomy, does not add new characters which the taxonomist can use; it merely realigns and gives back numerical data which have been gathered by other means. Moreover, as numerical taxonomy exists today, it actually restricts the kinds of information that can be used. As seen below, no satisfactory method for quantification of non-numerical characters has been found. Until this obstacle is overcome, numerical taxonomy will neces-

sarily be biased in its scope, and will lose many characters which are considered important by most taxonomists.

Since numerical morphological characters of *Perezia* specimens were recorded on IBM cards for use in the taxonomic treatment (PART II), cards were available for a numerical taxonomic study. It was undertaken with two purposes in mind: as a possible way of presenting data about *Perezia* species in a new and perhaps slightly provocative manner; and, as a trial to learn and test the methodology and principles of numerical taxonomy.

The statistic chosen for use in this numerical taxonomy program was Mahalanobis' generalized distance D^2, in which

$$D_p^2 = \sum_{i=1}^{p} \sum_{j=1}^{p} (cov^{-1})_{ij} (\overline{X}_j - \overline{X}'_j)(\overline{X}_i - \overline{X}'_i)$$

where p is equal to the number of characters and $(\mathrm{cov}^{-1})_{ij}$ represents the inverted covariance matrix, cov_{ij}, and $\overline{X}_i$ and $\overline{X}_i'$ are the means for the primary groups X and X′ for character i.

This procedure was used for several reasons. First, a computer program was readily available (written and discussed by Minkoff, 1965). Second, this statistical method, recommended by Rao (1952) and Minkoff (1965), treats only continuous numerical characters, deals only with populations, and takes both variance and covariance into account. The distance D^2 is actually measured in units of variance between the primary groups with which it is dealing.

To determine how the various species (and in some cases confusing populations) would be grouped, on the basis of numerical characters alone, a series of computer programs was run using Mahalanobis' distance to measure the "taxonomic distance" between primary groups. The term *primary group* here refers to a group of specimens treated as a unit in a given run of the program. The primary groups were species, subspecies, or local populations of a single species, e.g., any distinct group of specimens whose placement by the computer would provide interesting information. The fact that "populations" are necessary in the computation of Mahalanobis' distance precluded the possibility of using individual specimens as the "operational taxonomic unit" (OTU),

as in the method of Sokal and Sneath (1963, p. 290). It is felt by most biologists that populations, and not individuals, should be stressed in systematics (Mayr, 1963; Stebbins, 1950).

Two options allowed by Minkoff in his program were used with each set of primary groups. Total covariance method used the total variance-covariance matrix in the calculation of D^2. This matrix was compiled by using the average variance of a character over all the primary groups being considered, i.e., in the computation of the covariance from the formula

$$\frac{1}{n-1}\sum (X_i-\overline{X}_i)(X_j-\overline{X}_{j.})$$

The values of $\overline{X}_i$ and $\overline{X}_j$ were the means for that character using all of the primary groups. In the second option, the value of each character for each of the primary groups was subtracted from the mean of that character (again $\overline{X}_i$ and $\overline{X}_j$) for only its own population and not the overall mean. Thus, the values of $\overline{X}_i$ and $\overline{X}_j$ change in the second option, depending on what primary group is being considered. The use of the total covariance method always gives higher values of cov_{ij} than the second option called the intra-group method.

Although it is thought to be more meaningful biologically (William Bossert, pers. comm.) to use the intra-group covariance matrix, little difference in the array of D^2 actually resulted from the two methods. In other words, although the absolute values (numerical values) of D^2 were different in the arrays using the two methods, the relative relationships of the populations remained more or less the same in the two methods. Some differences were of course produced. Part of the lack of greater differences in the D^2 arrays, using the two options, could have been due to the fairly consistent primary group size. Rao (1952, p. 364) gave a correction of D^2 for bias in the computation due to large differences in the primary group sizes. However, he stated that if $\left(\frac{n_1+n_2}{n_1n_2}\right)$ (where n = primary group size) is very nearly the same for all primary groups, the correction is trivial. The differences in the primary group sizes in the runs discussed were no greater than those used by Rao (1952), p. 358) in his example, which he considered to be negligible.

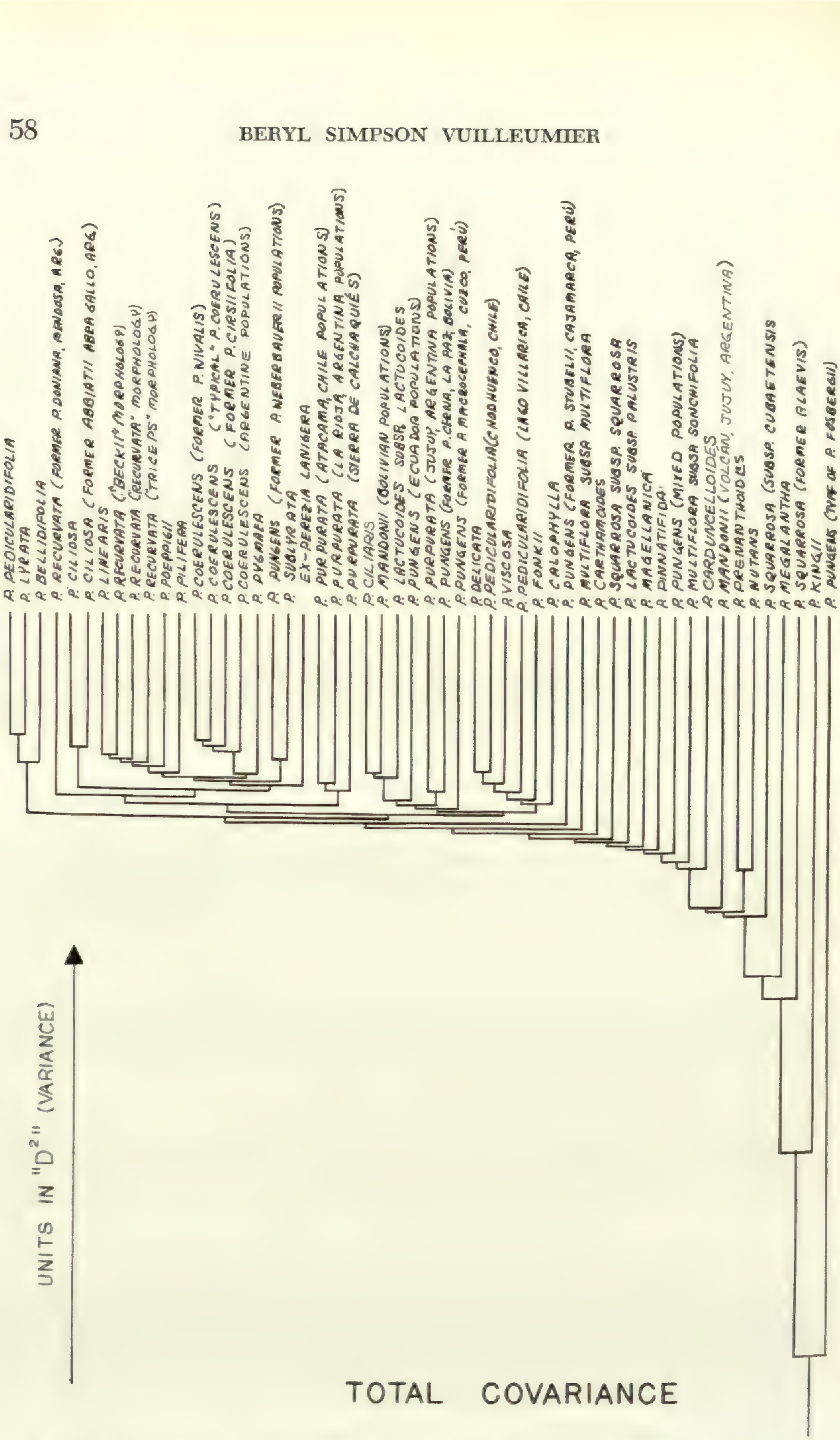


FIG. 14. Dendrogram of *Perezia* species based on Mahalanobis' distance (D^2) using the total covariance option (see text). The primary group on the far right appears very removed from the other groups partly because it consisted of only one specimen (i.e., 0 variance).

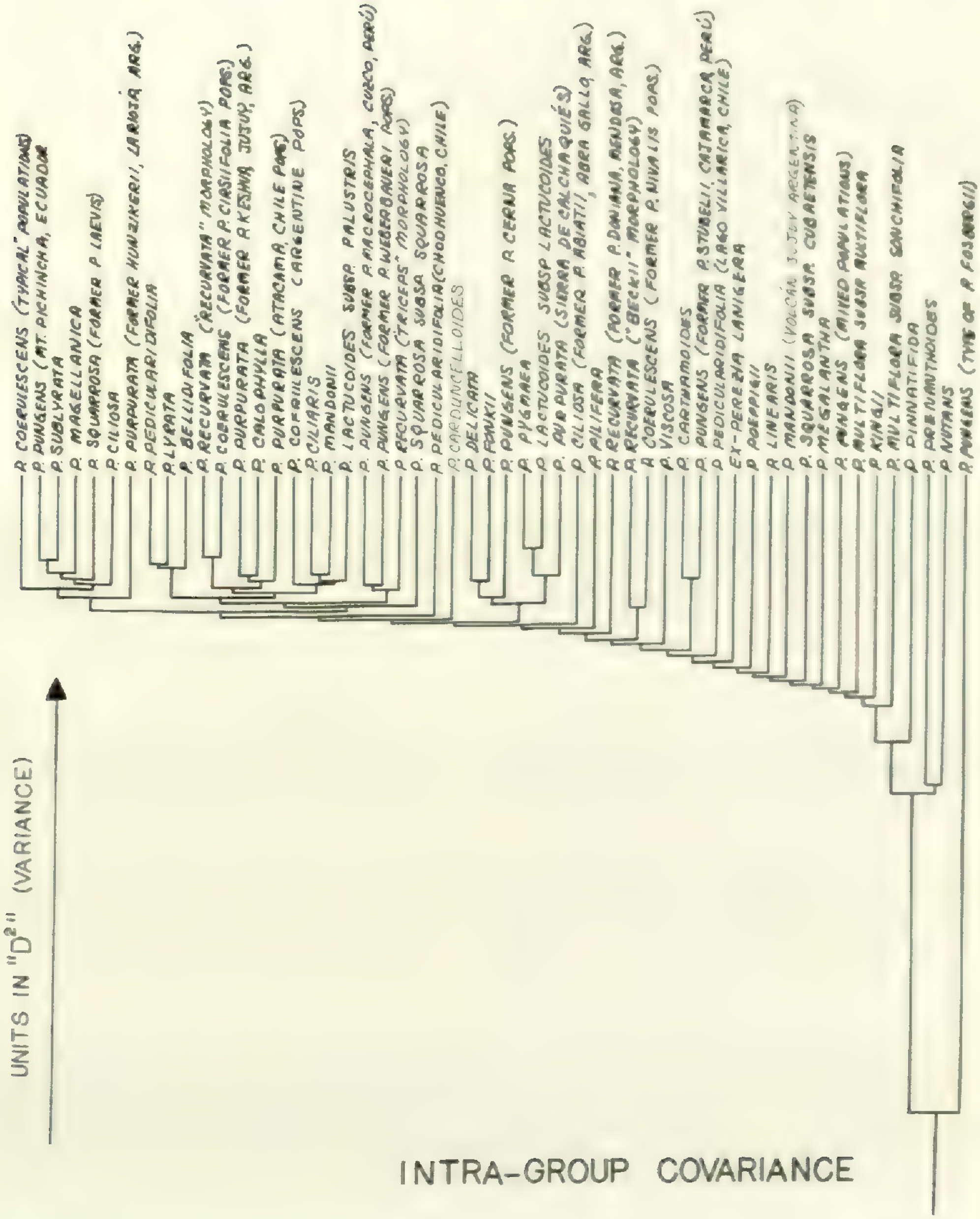


FIG. 15. Dendrogram of *Perezia* species based on Mahalanobis' distance (D^2) using the intra-group covariance option (see text). As in FIG. 14, the group on the far right appears very distant from the other groups because it consisted of only one specimen.

That the results from the two divergent methods agreed so well in essential points indicates that the program accomplished the task for which it was written. That is, it gave a measure, based on a series of continuous variables, of the distance between two primary groups (populations).

Of the two, the total covariance option actually conformed slightly better to the scheme of relationship arrived at by morphological data. There does not seem to be a satisfactory (logical or statistical) explanation for this. There is a likelihood that the slight differences between the two options were actually due to chance.

The computer generated D^2 matrices for the two options of the main program. Fifty-four primary groups representing species, subspecies, and biological populations were used. In the arrays of D^2, each of these groups was listed in order, and next to it a block of numbers composed of the distances (D^2) between that group and each of the other 53. Lack of space prevents giving the complete matrices, but the dendrograms (redrawn) for each option are presented in Fig. 14 and 15. Unfortunately, they distort much of the information given in the original matrices because of the manner in which they were constructed, i.e., the first two groups joined were the pair with the shortest distance (compared with all other possible pairs) between them, and then the next closest group to *either* of the original pair (depending on which distance was numerically smallest) was added next, and so on. Obviously, such a system provides no information about the group which was closest to the other member of the original pair of primary groups, or what the distance of a particular group x was to y. The artifacts due to the mechanical method of drawing the dendrograms also exaggerated the difference between the two options (Fig. 14 compared with Fig. 15). However, the dendrograms did reflect the difference present in the original matrices in that the picture of distances drawn from the total covariance matrix (Fig. 14) did conform better to a scheme of relationships based on morphology than did the picture drawn from the intra-covariance matrix (Fig. 15).

Smaller programs, the results of which are not given here, were run using populations of one species. In most cases, the sample size of the primary groups was so small that there was not enough variance present in various characters to allow an accurate com-

putation of D^2. In many of these small runs, a primary group of only one individual was used even though the program called for primary groups of more than one. Whenever a group of only one specimen was encountered in the program, it was disproportionately far away from the other groups. An example of this distortion can be seen in Fig. 14 and Fig. 15 where the group on the extreme right of both dendrograms (*P. pungens*, former type of *P. fosbergii*) appears very removed from the other groups. This group was the only one of the 54 used in the main program with one individual.

EVOLUTION OF THE SPECIES GROUPS

A synthesis of the data discussed above, obtained from morphology, anatomy, palynology, cytology, and chemistry, provides convincing evidence for the presence of six species groups in *Perezia* which have stemmed from three major evolutionary lines. Although the species can be clustered into six well-defined groups, it is more difficult to ascertain the historical relationships between them, because of the internal evolution undergone since their divergence. Clear-cut evolutionary lines are hard to trace between species also because characters have evolved mosaically (*sensu* Mayr, 1963) within individual species. However, some character states are obviously highly adapted to specialized conditions and can therefore serve as indicators of the direction of change of those characters. By combining the information from several such characters with that provided by cytology and chemistry, some relationships and evolutionary trends emerge.

This combined approach has, in my opinion, provided a firm basis for the taxonomy arrived at here and represented schematically in Fig. 16 and 17. The two figures attempt to give a conceptual picture. The first does so diagramatically and the second by illustrating representative species and the relationships between the different species and species groups. Each species group will be briefly characterized below and its postulated origin and subsequent radiation discussed to amplify the scheme presented in the figures. Many of the data concerning paleoclimatological, geological, and botanical changes mentioned here will be elaborated upon more fully in a later paper.

By all criteria, one of the most distinctive and well-defined

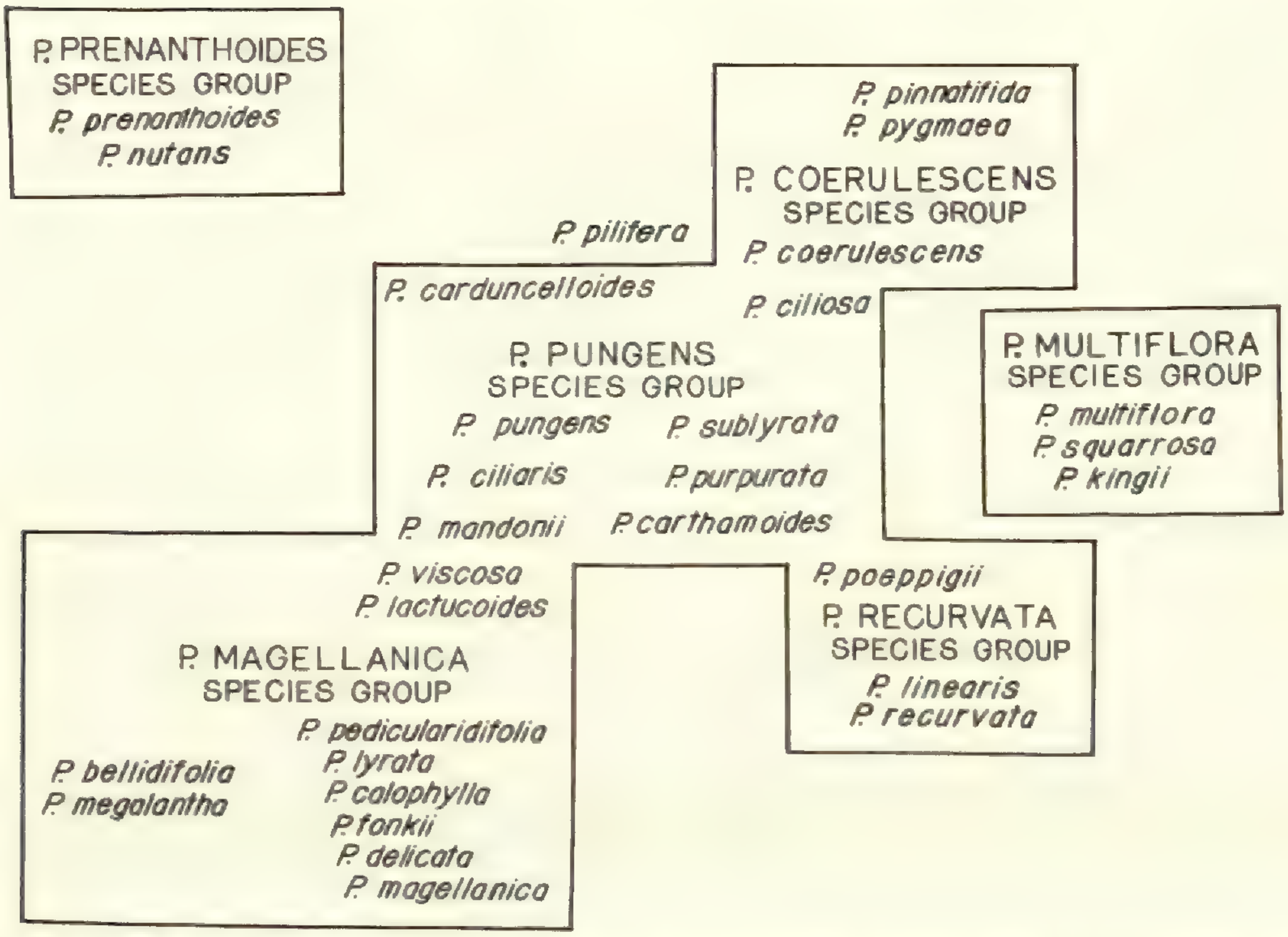


FIG. 16. Schematic representation of the relationships between the species and species groups of *Perezia* sect. *Perezia*. (See FIG. 2 for the distribution of the groups.)

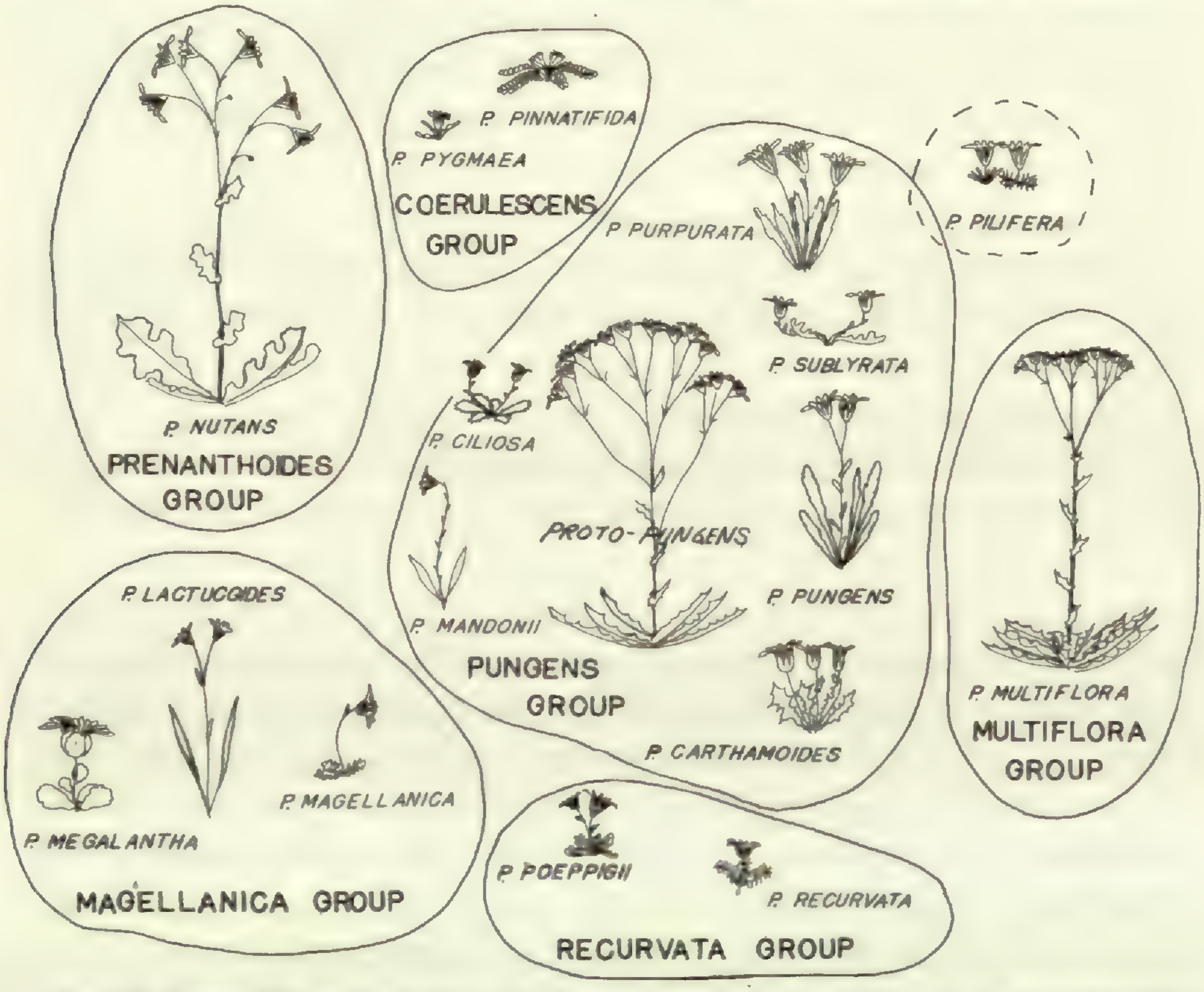


FIG. 17. Pictorial representation of selected species of *Perezia* sect. *Perezia* showing the type of habit found within each species group (compare with TABLE 2).

species groups centers around *Perezia multiflora*. All of the species of this assemblage are found exclusively, or have populations, in the Paraguay-southern Brazil-Uruguay basin, although *P. multiflora* itself has its main center of distribution in the high, dry puna of Perú and Bolivia. The three species which comprise this alliance share the unusual (within this section) characters of silky, copper-colored achenial trichomes, hemispherical involucres, and a reduced number of involucral bracts. The eastern subspecies of *P. multiflora* and *P. kingii* approach some species of *Cleanthes* D. Don and *Trixis* R. Br. (two genera of the same subtribe) in habit because of their highly branched flowering stems and numerous heads in a paniculate arrangement.

If the trend of evolution within *Perezia* sect. *Perezia* (and even within the subtribe *Nassauviinae*) has been from an ancestral type like *Trixis*, as suggested by Small, then the *P. multiflora* group would presumably be closer in morphology to the ancestral stock than any other extant group in the genus. The presence of a chromosome number of $2n=8$ for *P. squarrosa* subsp. *cubaetensis* and $2n=16$ for *P. multiflora* (compared with $2n=24$ [26] for all other species which have been counted) also points to this group as primitive. However, its species have several characters which are obviously advanced, such as compacted head clusters, reduced involucre and head size, taproots rather than rhizomatous rootstocks, and spinose foliage. *Perezia multiflora* itself has become weedy and is the only species in the section which can colonize quickly and efficiently.

Therefore, although retaining the lowest chromosome numbers in the genus, including the probable base number of $n=4$, the *Perezia multiflora* group does not appear to represent the basal complex in the section, nor does it appear to have given rise to any of the other groups. Rather, it seems to be a closely knit cluster of species which radiated in southeastern Brazil from a very early offshoot of the main ancestral stock. The progenitor of this group underwent speciation by splitting in the Paraguay-Brazil-Uruguay basin and *P. multiflora* probably migrated westward into the Andes at a later time.

A second, early, major line seems to have culminated in the two closely related species of the *Perezia prenanthoides* group, both endemic to the *Nothofagus* forests of southern South America. Morphologically, these two very similar species form the most

unique group of the section. Plants of both species are large, foliaceous herbs with showy open clusters of numerous magenta heads, broad, soft, basal leaves, and achenes with dense coverings of amber-colored trichomes. (PLATE 1–4). Unfortunately, no chromosome counts are available for either species of this group. Superficially, *P. nutans*, one member of this group, resembles *P. nana* A. Gray, a member of the North American section *Acourtia*. *Perezia nutans* is the only species of the South American section that looks at all like any of its northern hemisphere counterparts.

Its large acaulescent habit, loose paniculately arranged heads, and montane forest habitat—all considered primitive characters—indicate that the *Perezia prenanthoides*, like the *P. multiflora* group, was an early offshoot from the ancestral stock and has retained many characters of the ancient type. However, the evolutionary histories of these two early lineages have apparently been completely different. The ancestor of the *P. multiflora* group, as outlined above, underwent speciation by splitting in the open woodlands of southern Brazil. In contrast, the *P. prenanthoides* group seems to be the product of a long, relatively uneventful period of phyletic evolution prior to the Pleistocene, during which it became more and more specialized to life within the *Nothofagus* forest. The two present species appear to have been recently separated, probably during the Pleistocene. During the glacial periods, a tongue of ice and enormous amounts of glacial outwash covered the longitudinal valley at the latitude of the Río Bío Bío (37°S) and effectively cut the forest belt along the slopes into a northern and a southern component. The two members of the *P. prenanthoides* group, like many other Chilean forest species, now show distributional limits at about this latitude. The pre-Pleistocene evolutionary pattern of the *Nothofagus* forest inhabiting species of *Perezia* is parallel to that found in some bird and frog genera endemic to the southern beech forests (Vuilleumier, 1967, 1968).

A number of species with varying degrees of specializations make up the rather heterogeneous *Perezia pungens* species group. Although some of these species have advanced characters, such as petioled leaves and glabrous achenes, the group as a whole, and *P. pungens* in particular, possesses all of the characters which appear to be unspecialized in the genus. This plexus of species

seems to be the modern remnant of a generalized assemblage which was at the base of the third major evolutionary line. In addition to its own internal evolution, this group seems to have provided the stocks which gave rise to the three remaining species groups now present in the section.

In northern Perú, in the upper reaches of the humid montane forests of Cajamarca and Amazonas, there are populations referable to *Perezia pungens*. These populations, isolated from others of *P. pungens*, are particularly similar in habit to *P. multiflora* and *P. prenanthoides*. Thus, there are members of three exceedingly divergent and widely disjunct species groups which show similarities in a primitive type of large, caulescent, polycephalous growth form. In distribution, these three groups, the *P. multiflora*, the *P. prenanthoides*, and the *P. pungens*, are found in southeastern Brazil, the *Nothofagus* forests of southwestern Patagonia, and the eastern slopes of the central Andes respectively. These same three disjunct geographical areas show other floristic relationships which suggest an ancient connection (i.e., *Araucaria*, *Podocarpus*, *Chusquea*). It appears likely (Gerth, 1941) that a warm subtropical forest covered most of South America during the early Tertiary (Cretaceous to Oligocene). A differentiation of this uniform forest began to occur in the mid-Tertiary. A new floristic assemblage developed from a combination of the indigenous southern flora and the Austral-Antarctica flora (*Nothofagus*, *Araucaria*, *Podocarpus*, *Proteaceae*, etc.) in the southwest, while in the west, the forest became more open and savanna-like. Despite this differentiation, it is probable that there was fairly continuous forest (although of changing composition) from southern Chile north to Perú, and east across northern Argentina until the end of the Miocene or beginning of the Pliocene. In the Pliocene, increased aridity (Groeber, 1936) isolated the forests in southern Patagonia from those in Perú and southeastern Brazil.

It is my suggestion that *Perezia* arose as a leafy, branched, perennial herb during the early mid-Tertiary in open warm forests. As the forests were separated, three main fragments of the ancestral stock were isolated: one in southeastern Brazil, one in southern Patagonia, and one on the montane slopes of the central, rising, Andes. The South American *Perezia* could not have arisen in the high Cordilleran puna nor the Patagonian steppe because these dry, cold habitats as they are today did not exist

much before the Pleistocene (Berry, 1919, 1922 a, b, 1937 a; Gerth, 1941; Ahlfeld and Braňisa, 1960). Not only are these habitats recent, but the species of *Perezia* which occur in them are advanced morphologically and have specializations for xerophytic conditions.

In addition to *Perezia pungens*, there are nine other species in the *P. pungens* group, many of which have become specialized in various characters accommodating themselves to the different ecological niches in the central Andean puna. Migrations from different segments of this group have led to secondary radiations culminating in the three more recently derived species groups (PLATE 1–1 to 1–3).

In the Chile-Argentine Andes, both above and fingering into the *Nothofagus* forest, the *Perezia magellanica* group occurs. This assemblage has the largest number of species in the section, and consists of small rosette plants, generally with monocephalous flowering stems, and achenes with long, dense double hairs (PLATE 1–5). Two species of this group (*P. viscosa* and *P. lactucoides*) are somewhat different from the others because of their polycephalous flowering stems and their approach, in gross morphology, to *P. ciliosa* and *P. mandonii* of the *P. pungens* group.

Because the southern high Andes are young (final uplift at the end of the Pliocene, Brüggen, 1950), and because most of the mountains were completely covered by ice several times during the Pleistocene (Caldenius, 1932; Brüggen, 1950; Polanski, 1965), the present distributional pattern of the species on extra-forest (above timberline) mountain peaks could not have been formed prior to the Pleistocene. The fact that there are numerous species, all very similar morphologically, most with restricted ranges, and some capable of natural hybridization, also attests to their recent origin and distribution. This type of geographic distribution of endemic and restricted species on mountain peaks suggests a cause parallel to that which has been proposed for the Scandinavian mountains (Hultén, 1937, 1965; Frenzel, 1968).

There were probably two distinct kinds of barriers which led to the original separation of populations of the *Perezia magellanica* group. The most obvious kind of barrier present in the Pleistocene during glacial periods was the ice itself. Undoubtedly some small populations survived in refugia within, or along the margins of, the ice sheets. However, a more probable kind of barrier

occurred during the interglacials. At the present time, which is an interglacial, the species adapted to alpine habitats above tree line are separated from one another by stretches of unsuitable habitat on the sides of the mountains and in the valleys. The populations on peaks are thus effectively isolated by expanses of forest. During glacial periods, the ice spread down the sides of mountains and across intermontane valleys. At the border of the ice was a zone of the same type of alpine (or tundra) habitat which had previously existed only on mountain peaks above timberline and below the snow (ice) line. Low altitude species not adapted to such harsh environments were eliminated or migrated north to warmer climates. The ice, therefore, had the effect of lowering the vegetation zones to the point where there was continuous alpine or tundra habitat across intermontane valleys, allowing high altitude species to migrate across these valleys.

As the ice ages waned, and the warmer interglacials replaced them, the ice retreated, taking with it its border of alpine habitats. Concomitantly, tree species reinvaded the valleys as the climate warmed. The net effect was that species adapted to cold tundra habitats essentially retreated up mountain peaks and were restricted to areas above treeline. A species which was continuous across a valley during a glacial period could easily have left populations isolated on neighboring peaks when the interglacials allowed the re-expansion of the forests. These populations would have the potential for speciation during interglacials when populations were geographically isolated. Since several different glacial advances occurred, there was opportunity for a series of periods of alternating migration and restriction. This rapid succession of expansions followed by isolation could easily have led to the pattern seen today in the *Perezia magellanica* group of several species, all closely related, and limited in distribution.

The most specialized, although probably not the most recently derived South American species group, is the *Perezia recurvata* group. Within this assemblage there is a nice evolutionary sequence, discernible from the relatively generalized *P. poeppigii* to the very highly specialized *P. recurvata*, i.e., from a loose, broad, flat-leaved habit to a highly compact, basally branched cushion plant with recurved, needle-shaped leaves (PLATE 2–4). The three species of this group share the common characters of a special type of achenial trichome (Fig. 3–2), large, turbinate

capitula, and stiff, lanceolate bracts. The reduction in leaf surface with stomata in *P. linearis* and *P. recurvata,* and the recurving of the leaves in *P. recurvata* show progressive steps in the adaptation of these species to the xerophytic conditions of the Patagonian plateau.

Part of the speciation in this group is probably attributable to isolation during glacial maxima, when populations were forced north or eastward by the encroaching ice or restricted to refugia. Chemical evidence, supported by some morphological similarities, indicates that *Perezia recurvata* and its allies are most closely related to *P. carthamoides,* a member of the *P. pungens* group. The affinities, and probable derivation of the *P. recurvata* complex from a segment of the *P. pungens* alliance emphasizes the central position as an ancestral plexus of the species associated with *P. pungens.*

A group of taxa, the *Perezia coerulescens* complex, is centered in the altiplano of Perú, Bolivia, and northwestern Argentina. All three of these species have adapted to the bizarre xerophytic conditions of high tropical mountains (e.g., see Troll, 1959) as evidenced by their reduced stature and compact rosettes tightly appressed to the ground with the heads hidden among the leaves (PLATE 2–1 to 2–3).

Available information indicates that this group is the most recently differentiated of the section. Morphologically, the species are very similar, leading to taxonomic confusion. In many ways, the group exhibits the characters of a hybrid complex rather than a species group. Yet, although there is evidence of hybridization in some localities, there seem to be distinct non-interbreeding species in other areas. The assemblage is obviously in a period of active speciation with incomplete reproductive isolation having been achieved. Whether the course of evolution will lead to reinforcement of isolating barriers, or to the submergence of the species will probably be determined in large part by the amount of future disturbance of their habitats by man.

Morphological and chemical evidence suggest that the *Perezia coerulescens* complex is related to *P. purpurata* of the *P. pungens* group. The affinities of *P. coerulescens* and its allies to a species related to *P. pungens* once more show how the *P. pungens* group is the focal point of relationships for the three most recently divergent groups.

To summarize, the ancestral type of the section was probably a relatively large, leafy, perennial herb with a rhizomatous rootstock and a loose panicle of heads. The most likely chromosome number was $2n=8$, and the karyotype was presumably composed of large, metacentric chromosomes. This early *Perezia* would have grown in open, cool subtropical (or warm temperate) forests. From this basal stock, three major lineages diverged, beginning in the mid-Tertiary. One of these lines, established in the southeastern Brazil lowlands, underwent a minor radiation leading to the three species of the *Perezia multiflora* group. A second line became increasingly adapted to the dense *Nothofagus* forests in which it underwent a long, relatively uneventful period of phyletic evolution. A recent separation of populations by a glacial barrier initiated the speciation of the two closely related species now found in the *P. prenanthoides* group.

The third major line, which inhabited the eastern montane slopes, radiated into the habitats which opened up as the Andes were increasingly uplifted. Over a period of time, a plexus of species was formed due to the isolation of populations on different ranges (or in different valleys) by unsuitable intervening terrain. From segments of this complex, three new lineages diverged. One colonized southward along the Andes in the late Tertiary, becoming established on several southern peaks. During the Pleistocene glaciations, these populations were subjected to alternating periods of expansion and isolation. Migration was permitted during glacials when the ice was low enough to produce a continuous band of alpine habitat from one mountain to another. Restriction of ranges occurred in interglacials as the forest reinvaded the intermontane valleys, making them unsuitable for alpine species. Local selection pressures on different mountains acting on isolates from three interglacial periods resulted in a rapid multiplication of species and produced the numerous, closely related taxa of the *Perezia magellanica* group.

Another segment of the *Perezia pungens* alliance, adapted to the increasingly xerophytic conditions of the late Tertiary, invaded the southeastern Andes and the Patagonian steppe. The three species of the *P. recurvata* group which resulted from a radiation of this stock still show an evolutionary sequence from a species of the dry Andean valleys to one of the Patagonian steppe. Within *P. recurvata* itself, isolation of populations in the

Pleistocene by encroaching ice tongues and innumerable streams of glacial outwash led to a pattern of complicated geographical variation when the isolates again came into contact during interglacial periods.

The third evolutionary line, culminating in the *Perezia coerulescens* group, arose from an ancestral stock derived from the *P. pungens* group which had become adapted to the conditions of the very high puna. The formation of the three species of the *P. coerulescens* group must be exceedingly recent because the specialized high tropical habitats in which they occur became available for colonization only at the end of the Pliocene or beginning of the Pleistocene. Differentiation of populations occurred later in the Pleistocene when isolation was effected by glacial ice and a complex series of lakes across the altiplano. Whether the isolation was sufficient to allow the development of effective reproductive barriers between the three taxa is still disputable. There does seem to have been enough separation to have permitted at least partial speciation. There is some evidence that interspecific barriers in this group are being broken down because of the disturbances of the altiplano habitats by man.

TAXONOMY

PEREZIA Lagasca, Amoen. Nat. 31. 1811.

Type species: *Perdicium magellanicum* L.f.

Clarionea Lag. ex de Candolle, Ann. Mus. Hist. Nat. Paris **19**:65. 1812. Type species: *Perdicium magellanicum* L.f. An illegitimate name because it was superfluous when published.

Clarionea Cassini, Opus. Phytol. **2**:165. 1826. non *Clarionea* Lag. ex DC. Type species:*Perdicium lactucoides* Vahl. An illegitimate name because it was a later homonym of *Clarionea* Lag. ex DC.

Clarionia D. Don, Trans. Linn. Soc. Ser. I **16**:204. 1830. Presumably an orthographic variant of *Clarionea* Lag. ex DC.

Clarionema Philippi, Linnaea **28**:717. 1858. Type species: *Clarionema humilis* Phil.

Homoianthus DC. Ann. Mus. Hist. Nat. Paris **19**:65. 1812. Type species: *Chaetanthera pungens* Humboldt & Bonpland.

Homanthis Humboldt, Bonpland & Knuth, Nov. Gen. Sp. Pl. **4**:12. 1820. Type species: *Chaetanthera pungens* H&B. An illegitimate name because it was superfluous when published.

Homoeanthus Sprengel, Syst. Veg. 3:503. 1826. An orthographic variant for *Homoianthus* DC.

Heteranthus Cassini, Dict. Sci. Nat. **21**:110. 1821. An admitted orthographic change for *Homoianthus* DC.

Isanthus DC. Prodr. **7**:63. 1838. An invalid name listed in synonymy with *Homoianthus* by de Candolle.

Dumerilia Lessing, Linnaea **5**:13, 1830. non *Dumerilia* Lag. ex DC. Type species: *Drozia Humboldtii* Less. An illegitimate name because it was a later homonym of *Dumerilia* Lag. ex DC.

Scolymanthus DC. Prodr. **7**:63. 1838. An invalidly published name listed only by de Candolle in synonymy with *Homoianthus* DC.

Stenophyllum Less. Synop. Comp. 412. 1832. Type species: *Perezia recurvata* (Vahl) Less. This name is frequently listed as a synonym of *Perezia,* but it was actually used only as a sectional name by Lessing in *Perezia.*

Drozia Cassini, Opus Phytol. **2**:170. 1826. Type species: *Drozia dicephala* Cass.

Acourtia D. Don, Trans. Linn. Soc. Ser. I. **16**:203. 1830. Type species: *Acourtia formosa* D. Don.

Pogonura DC. ex Lindley, Introd. Nat. Sys. ed. 2. 263. 1836. A *nomen nudum* attributed to de Candolle by Lindley, but apparently never published by de Candolle.

Proustia section (3) *Thelecarpaea* DC. Prodr. 7:27. 1838. *Proustia reticulata* Lag. ex D. Don.

Perennial leafy caulescent or scapose herbs 2 cm to 3 m tall. Rootstocks rhizomatous, tuberous, or a simple taproot; some with tufts of brown wool on the basal caudex. Stems terete in cross section, glabrous or pubescent with multicellular glandular trichomes; sometimes striated; often reddish in color. Stem leaves absent to very numerous, scattered up the stem, scale-like to broadly oblong or ovate, mucronate, acute or obtuse, entire, dentate, lacerate or ciliate, clasping; usually reticulately veined; coriaceous to chartaceous; glabrous to densely pubescent. Basal leaves in a variable rosette,

linear, lanceolate, lyrate, spathulate, oblong or ovate, acute to obtuse, sometimes with recurved margins, usually with a flat blade, margins entire, ciliate, dentate, pectinate, lacerate, or pinnately parted; attenuate at the base or with a distinct petiole; 2 mm to 20 cm wide, and 7 mm to 32 cm long; surface coriaceous to chartaceous, glabrous, punctate or pubescent with multicellular trichomes. Heads in a many-branched panicle or cyme or borne individually. Capitula campanulate, homogamous. Involucre obconic, turbinate, or hemispherical, variable in size from 9 mm to several centimeters long and wide, composed of bracts in three or more series (except in two species where there are two rows). Outer bracts very variable, linear lanceolate to orbicular, mucronate to obtuse, entire to lacerate, glabrous to densely pubescent, green to red-purple, often with scarious margins. Inner bracts lanceolate to oblanceolate, mucronate to obtuse, entire or slightly dentate, sometimes apically pubescent, green to red-purple, usually scariously margined. Pappus setose, in some North American species clavate at the apex, white, brown or reddish in color. Florets all similar, hermaphroditic, fertile, bilabiate with the outer three lobes fused into a strap-shaped or elliptic ligule and the inner two lobes shorter, separate and curled; color variable, blue, brown, yellow, cream, mauve, pink, crimson, magenta, lavender, or purple; several floret colors sometimes present on different plants of the same species. Capitula radiate or with the corollas all equal. Anthers with acute terminal appendages and long acuminate basal appendages. Style globose at the base, terete, bifurcate at the apex. Style branches truncate with papillae on the edges. Achenes broadly or narrowly elliptic, inconspicuously ribbed, glabrous, glandular-pubescent or with long double trichomes. Receptacle flat or slightly convex, glabrous, with scattered glandular or long trichomes, or densely tufted with long trichomes around the points of achene attachment. Pollen tricorporate, spherical to slightly prolate, surface smoothly reticulate.

KEY TO THE SECTIONS OF PEREZIA

A. Caudex with a tuft of dense woolly rust-colored trichomes; capitula not radiate; involucral bracts stiff; florets lavender-pink, or white ..... section *Acourtia.*

A. Caudex glabrous; capitula radiate; involucral bracts frequently soft, but sometimes rigid; florets usually blue, sometimes yellow, magenta, pink, violet, crimson, rarely white ..... section *Perezia.*

Perezia Section Perezia

Perennial rosette herbs 2 cm to 1 m tall. Rootstocks rhizomatous, or tap root. Basal caudex glabrous or with a few scattered glandular trichomes. Basal leaves usually attenuate or clasping; in a few species petioled. Involucres turbinate to broadly hemispherical. Involucral bracts stiff and broadly scarious or soft and only slightly scarious. Capitula radiate. Pappus setose, never thickened at the apex. Florets blue, white, cream, yellow, coffee, purple, magenta, violet, red, or crimson. Corolla usually glabrous or in a few cases with glandular trichomes on the neck and the under surface of the ligule.

KEY TO THE SPECIES

A. Plants with leafy flowering stems, more than two capitula per flowering stem, (B).

B. Basal leaves spiny, ciliate, or with small dentate segments; capitula few or in a tight inflorescence, not showy; florets blue, white, cream, yellow, rarely pink, (C).
C. Basal leaves sessile (or lacking) and ovaries covered with a very dense covering of copper-colored double hairs, (D).
D. Capitula longer than 10 mm; pappus brown, (E).
E. Florets bicolored with yellow on the inner part of the corolla tube and the inner petals; heads often congested . . . . . 1. *P multiflora.*
E. Florets monochromatic; heads in a loose panicle . . . . . 2. *P. squarrosa.*
D. Capitula less than 10 mm long; pappus pure white. 3. *P. kingii.*
C. Basal leaves petiolate; achenes with a moderate covering of blond trichomes, glabrous, or with scattered trichomes, (G).
B. Basal leaves with large, obtuse, soft, doubly dentate teeth; capitula in a loose inflorescence, showy; florets magenta, (F).
F. Capitula hemispherical, upright . . . . . 4. *P. prenanthoides.*
F. Capitula turbinate, nodding . . . . . 5. *P. nutans.*
G. Basal leaves with undulate margins or blunt teeth, (H).
H. Flowering stems decumbent, capitula elongate, outer bracts entire . . . . . 9. *P. sublyrata.*
H. Flowering stems upright, capitula campanulate or shortly turbinate, (I).
I. Achenes with dense glandular hairs or dense double hairs; foliage with dense glandular trichomes, (J).
J. Achenes with dense glandular trichomes. 6. *P. pungens.*
J. Achenes with dense silky double hairs . . . . . 22. *P. calophylla.*
I. Achenes with sparse strigose trichomes, or glabrous; foliage with only a few scattered trichomes, (K).
K. Outer bracts foliaceous; florets yellow or violet . . . . . 8. *P. carduncelloides.*
K. Outer bracts stiff, spiny or entire; florets blue, (L).
L. Plants monochephalous; bracts smooth margined; stem leaves reduced in size . 10. *P. mandonii.*
L. Plants di- to polycephalous; bracts generally spiny; stem leaves not scale-like . 7. *P. ciliaris.*
G. Basal leaves with sharp teeth, lyrate in outline, (M).
M. Outer bracts densely pubescent with glandular trichomes . . . . . 12. *P. purpurata.*
M. Outer bracts glabrous or with very few scattered trichomes, broadly scarious . 14. *P. carthamoides.*
A. Plants with few, reduced stem leaves; capitula 1 or 2 per flowering stem, (N).
N. Achenes glabrous, with short sparse trichomes, or with glandular trichomes; receptacle glabrous or with scattered long trichomes, (O).
O. Leaves linear, linear-lanceolate, or needle-shaped due to recurving of the margins, (P).
P. Leaves with recurved margins . . 30. *P. recurvata.*
P. Leaves with flat lamina, (Q).
Q. Leaf margins smooth; leaves petioled . . . 10. *P. mandonii.*
Q. Leaf margins ciliate or with long white spines, (R).
R. Leaf margins densely and evenly ciliate. 29. *P. linearis.*

R. Leaf margins with scattered long soft white spines .... 11. *P. pilifera.*

O. Leaves lanceolate to ovate in outline, dentate, undulate, or spiny along the margins, (S).

S. Outer bracts pandurate or orbicular in outline, as long as, or longer than, the inner bracts, sometimes thickened at the apex and deeply toothed, (T).

T. Plants reduced; basal leaves deeply incised, segments rounded and conduplicate; capitula nestled among the leaves ..... 26. *P. pinnatifida.*

T. Plants tall, robust, upright, basal leaves dentate, with flat segments; flowering stems rising well above the rosette .... 18. *P. lyrata.*

S. Outer bracts lanceolate to ovate, shorter than the inner bracts, slightly toothed at the apex, (U).

U. Basal leaves with 3–4 deep, rounded segments; plants shorter than 3 cm ..... 27. *P. pygmaea.*

U. Basal leaves undulate or with numerous lobes or teeth; plants over 3 cm tall, (V).

V. Involucral bracts lanceolate, bright green in the center; flowering stems rising well above the basal rosette .... 10. *P. mandonii.*

V. Involucral bracts ovate, dark green or reddish in the center; flowering stems the same length as, or slightly longer than, the basal leaves, (W).

W. Outer bracts stiff, very scarious, deep red in the center and white along the edges. 12. *P. purpurata.*

W. Bracts soft, slightly scarious, entirely green or brown ..... 25. *P. coerulescens.*

N. Achenes with a dense covering of silky double hairs; receptacle with tufts of trichomes, (X).

X. Basal leaves with smooth or undulate margins (often absent in herbarium material of *P. lactucoides*); involucral bracts lanceolate, acute, (Y).

Y. Basal leaves petiolate ..... 16. *P. lactucoides.*

Y. Basal leaves attenuate at the base, (Z).

Z. Basal leaves ovate, outer bracts broadly scarious ..... 23. *P. bellidifolia.*

Z. Basal leaves spathulate in outline; outer bracts not scarious or with a narrow scarious margin, (a).

a. Flowering stems robust, bearing more than three stem leaves; ligules with glandular trichomes .. 15. *P. viscosa.*

a. Flowering stems delicate, bearing three or fewer stem leaves; ligules glabrous ..... 20. *P. delicata.*

X. Basal leaves deeply dentate, or deeply lobed (or needle-like and fleshy) with long soft white spines, (b).

b. Basal leaves and outer bracts with soft, long white spines .... 13. *P. pilifera.*

b. Basal leaves non-spiny, serrate, dentate, deeply lobed, or ciliate, (c).

c. Basal leaves and outer bracts evenly and densely ciliate .... 11. *P. ciliosa.*

c. Basal leaves dentate or lobate, (d).

d. Outer bracts spathulate, orbicular, or circular in outline (sometimes cordate), (e).
e. Outer bracts acuminate, cordate, purple; entire plant hispid ..... 24. *P. megalantha.*
e. Outer bracts spathulate or orbicular; plants with scattered glandular trichomes ..... 18. *P. lyrata.*
d. Outer bracts lyrate or lanceolate in outline, (f).
f. Flowering stems robust; outer bracts reddish, deeply incised, or stiff and entire, (g).
g. Outer bracts deeply incised; capitula hemispherical; plants with abundant glandular trichomes ..... 17. *P. pedicularidifolia.*
g. Outer bracts entire, very scarious; capitula broadly turbinate; plants with scattered trichomes ..... 12. *P. purpurata.*
f. Flowering stems delicate, bracts lanceolate, entire or slightly serrate, (h).
h. Outer bracts long and narrow, stiff, lanceolate, bright green, prominently scarious; florets cream, yellow, red or blue ..... 28. *P. poeppigii.*
h. Outer bracts shortly lanceolate, delicate, reddish in color, slightly scarious; florets white or blue, (i).
i. Heads very radiate; florets white; plants covered with long red trichomes ... 21. *P. magellanica.*
i. Heads slightly radiate; florets blue; plants with a few scattered colorless glandular trichomes ..... 19. *P. fonkii.*

1. Perezia multiflora (H. & B.) Less.

Tall robust leafy rosette plants 15–74 cm tall with a thick woody taproot. Stem round in cross section, striated, covered with multicellular glandular trichomes which are exceedingly dense under the capitulum. Stem leaves numerous, lanceolate, acute or mucronate, usually clasping; some scattered glandular trichomes on the surface. Basal leaves in a variable rosette, lanceolate, attenuate at the base, acute to mucronate, dentate–sometimes doubly so–with spiny segments; 7–35 mm wide, 3.1–37 cm long. Inflorescence a panicle of heads of 3–46 capitula; often more than one flowering stem per plant. Capitula campanulate, 11–25 mm wide, 10–22 mm long; upright. Involucre hemispherical; 9–23 mm wide, 7–18 mm long; composed of 2–4 rows of bracts. Outer bracts ovate, mucronate, spiny toward the base, 1–4 mm wide and 6–13 mm long; bearing dense multicellular glandular trichomes on the surface; often slightly scarious at the base; sometimes slightly reddish in color. Inner bracts lanceolate, mucronate, entire, 2–5 mm wide, 7–20 mm long, with multicellular glandular trichomes especially at the apex; broadly scarious along the margins and at the base. Pappus setose, white or reddish in color; 5–16 mm long; thick. Florets with a blue or white outer ligule and yellow inner part of the corolla tube and inner two petals; the capitula thus having the appearance of possessing blue ray florets and yellow disc florets. Outer florets 6–16 mm with ligules 1–11 mm; ligules frequently with glandular trichomes on the under surface; from 15–35 florets per head. Immature achenes 1–3 mm long with a dense covering of

silky red or blond trichomes. Mature achenes to 4 mm long, dark in color with fewer silky trichomes than the ovaries. Receptacles with dense tufts of long trichomes around the points of achene attachment.

KEY TO SUBSPECIES

Heads usually 9 or more per peduncle, florets bluish, basal leaves usually over 6 cm long. ..... 1a. *P. multiflora* subsp. *multiflora.*
Heads fewer than 9 per flowering stem, but several flowering stems sometimes present per rosette, florets white, basal leaves absent or if present usually shorter than 6 cm and with rounded segments ..... 1b. *P. multiflora* subsp. *sonchifolia.*

1(a). Perezia multiflora (H. & B.) Less. subsp. multiflora

Chaetanthera multiflora Humboldt & Bonpland, Pl. Aequin. **2**:168. Planche 135. 1809. Type: ECUADOR. Pichincha: Volcán Antisana (P).

Homanthis multiflorus (H. & B.) Humboldt, Bonpland & Knuth, Nov. Gen. Sp. Plant. **4**:14 (quarto edition). 1820.

Perezia multiflora (H. & B.) Lessing, Linnaea **5**:19. 1830.

Homoianthus multiflorus (H. & B.) de Candolle, Prodr. **7**:64. 1838.

Perezia multiflora (H. & B.) Less. var. *achalensis* O. Kuntze, Rev. Gen. **3**(2):167. 1898. Type: ARGENTINA. Córdoba: Sierra Achala de Córdoba al pie de Cerro Gigantes, 8–I–1887, *Hieronymus s.n.* (NY, Isotype GH).

Clarionea polycephala Cassini, Opus. Phytol. **2**:167. 1826. An illegitimate name because Cassini used it to replace the name *Chaetanthera multiflora* H. & B.

Perezia bidentata Meyen, Reise um die Erde **1**:470. 1834. Type: PERU. Puno: Talaram, 14000–15000 ft, IV–1831, *Meyen s.n.* (Photo GH of type at B).

Perezia acanthoides Hooker & Arnott, Comp. Bot. Mag. **1**:33. 1835. Type: ARGENTINA. Mendoza: without locality, *Gillies* (type not seen).

Perezia glomerata Rusby, Mem. Torrey Club **4**:214. 1895. Type: BOLIVIA. Cochabamba, 10000 ft, 1890 *Bang 736* (NY).

Plants tall, averaging 34 cm in height. Basal leaves usually in a dense rosette; usually over 6 cm long, spiny along the edges. Capitula usually 9 or more per flowering stem, clustered in a tight inflorescence (except in the Córdoba populations). Ligule 3 mm long, blue or whitish blue in color.

Chromosome number: $2n=16$ (Fig. 5–1).

Distribution: from southern Colombia south in the Andes through Ecuador, Perú, and Bolivia to extreme northern Chile and central Argentina (Fig. 18). Altitudinal range from 1000 m to 4500 m. Flowering from December to July.

Representative specimens: COLOMBIA. Cauca: Alto Volcán Puracé, 3000 m, 7–XI–1948, *Agredo, Molina, Barkley 18Ca082* (US), 3700 m, II–1938, *von Sneidern* 1958 (GH), 2600–3000 m, *Lehman 5670* (F, GH), Cordillera Central, Páramo de Puracé, South of Volcán San Francisco, 3450–3500 m, 23–VI–1943, *Cuatrecasas 14684* (F). ECUADOR. Pichincha: Mt. Pichincha, 3800 m, *Mille 748* (GH). Cotopaxi: Cordillera Occidental, Cordillera de Angamarca y Zumbagua, Páramo de Melen, 3700 m, 15–16–VII–1959, *Barclay & Juajiboy 7984* (US). Tungurahua–Napo-Pastaza: Roma Páramo al este de San José de Poalo, 3300 m, 31–VIII–1959, *Barclay & Juajiboy*

9231 (US). Chimborazo: Volcán Chimborazo, VI–1964, *F. Vuilleumier 1* (GH). Cañar: near El Tambo, 9500–10000 ft, 5–VII–1945, *Camp E4011* (GH); 5 km south of Cañar, Cerro Beieran (Páramo de Curiquinga), 3570–3630 m, 29–I–1945, *Fosberg & Giler 22657* (US). PERU. Lima: Cerro Colorado near Antaicocha, east of Canta, 3800–4100 m, 20–VI–1925, *Pennell 14652* (GH); Río Blanco, 12000 ft, 8–19–V–1922, *Macbride & Featherstone 654* (GH). Junín: Chicla 12–13000 ft, 21–V–1882, *Ball s.n.* (GH). Puno: Araranca, 4100–4200 m, 21–VI–1925, *Pennell 13429* (GH); Huancane, Moho, 3125 m, 19–XII–1919, *Shepard 109* (GH). Huancavelica: Huancavelica, quebradas west from Huancavelica, 3900 m, 10–III–1939, *Stork & Horton 10846* (GH); Machacchuay, between Conaica y Tinyacella, 3850–3900 m, 28–III–1952, *Tovar 867* (GH); Tansiri, Huaytanayoc, cerca a Manta, 4400–4500 m, 31–III–1953, *Tovar 1174* (GH). Arequipa: without locality, 2000–3600 m, 3–II–1912, *Guenther & Buchtien 911* (HBG). Tacna: Tacna, Cordillera de Volcán Tacora, Chislluma, 4500 m, IV–1926, *Werdermann 1142* (GH, US). BOLIVIA. La Paz: La Paz, V–1890, *Buchtien 4811* (GH); Tiaguanaco, 3860 m, III, *West 6374* (GH); Larecaja, between Pongo and Anilaya, 3600–3900 m, IV–1857, *Mandon 26* (GH). Oruro–Cochabamba: Bandorani, 5–II–1949, *Brooke 5208* (NY). Cochabamba: Cercado, Caluya, 3800 m, 22–IV–1920, *Steinbach 4065* (GH); Chapare, Cuchicancha, 3300 m, 17–III–1929, *Steinbach 9631* (GH). Tarija: Escayache bei Tarija, 3600 m, 30–I–1904, *Fiebrig 3018A* (GH). ARGENTINA. Jujuy: near Tilicara, Chorru Valley, 12000 ft, 2–13–1939, *Balls s.n.* (US); Casapalca, 3200 m, 1–III–1940, *Burkart & Troncosa 11737* (SI); Tilcara, Quebrada de Ventura, 3800 m, 3–III–1961, *Cabrera & Hernandez 13969* (GH). Salta: Santa Victoria Lizoite, 3340 m, 1–IV–1940, *Meyer & Bianchi 33037* (GH); Quachipas, Alemania 1600 m, 18–XII–1929, *Venturi 9944* (GH). Tucumán: Anfama, XII–1871, *Lorentz 406* (CORD); Sierra de Tucumán, Ciénega, 10–I–1874, *Lorentz & Hieronymus 712* (CORD); Chicligasta, La Cascada a las Luevas, 3000 m. 10–III–1949, *Meyer 14900* (LIL), Estancia Santa Rosa, Punto La Cueva, 3800 m, 14–III–1924, *Venturi 3176* (GH); Estación Las Pavas, 28–XI–1926, *Venturi 4662* (GH, SI); Tafí, entrada de la "Angostura" cerca Tafí del Valle, 1900 m, 24–I–1950, *Sleumer 186* (LIL). Catamarca: Andalgala, 12–IX–1915, *Jorgensen 1326* (GH). Córdoba: Copina, 29–XII–1935, *Burkart 7513* (SI); Pampa de Achala, quebradas al oeste, 2000 m, 22–II–1965, *Cabrera & Solbrig 16619* (GH); Sierra Grande, 10 km below El Cóndor, 1000 m, 16–XII–1938, *Goodspeed 17236* (GH); between Cañada Larga and la Pumilla, 7–XII–1870, *Hieronymus 605* (CORD); camino al Cerro Los Gigantes, 25–III–1886, *Kurtz 3841* (CORD). San Luis: El Mongote, 2–II–1911, *Pastore 37* (SI). CHILE. Tarapacá: Arica, Portezuelo de Chapiquina, 4200 m, 29–III–1961, *Ricardi, Marticorena & Matthei 334* (CONC).

The range of *Perezia multiflora* far exceeds that of any other species of the section as is clearly shown by a comparison of Fig. 18 with the other distribution maps. Its distribution (including both subspecies) covers a north-south distance of almost 4800 km and an east-west distance of 3200 km. It appears that part of the wide range of *P. multiflora* is due to the distribution of its achenes by water. Field observations and collection data indicate that plants tend to grow near streams or ditches which are cut

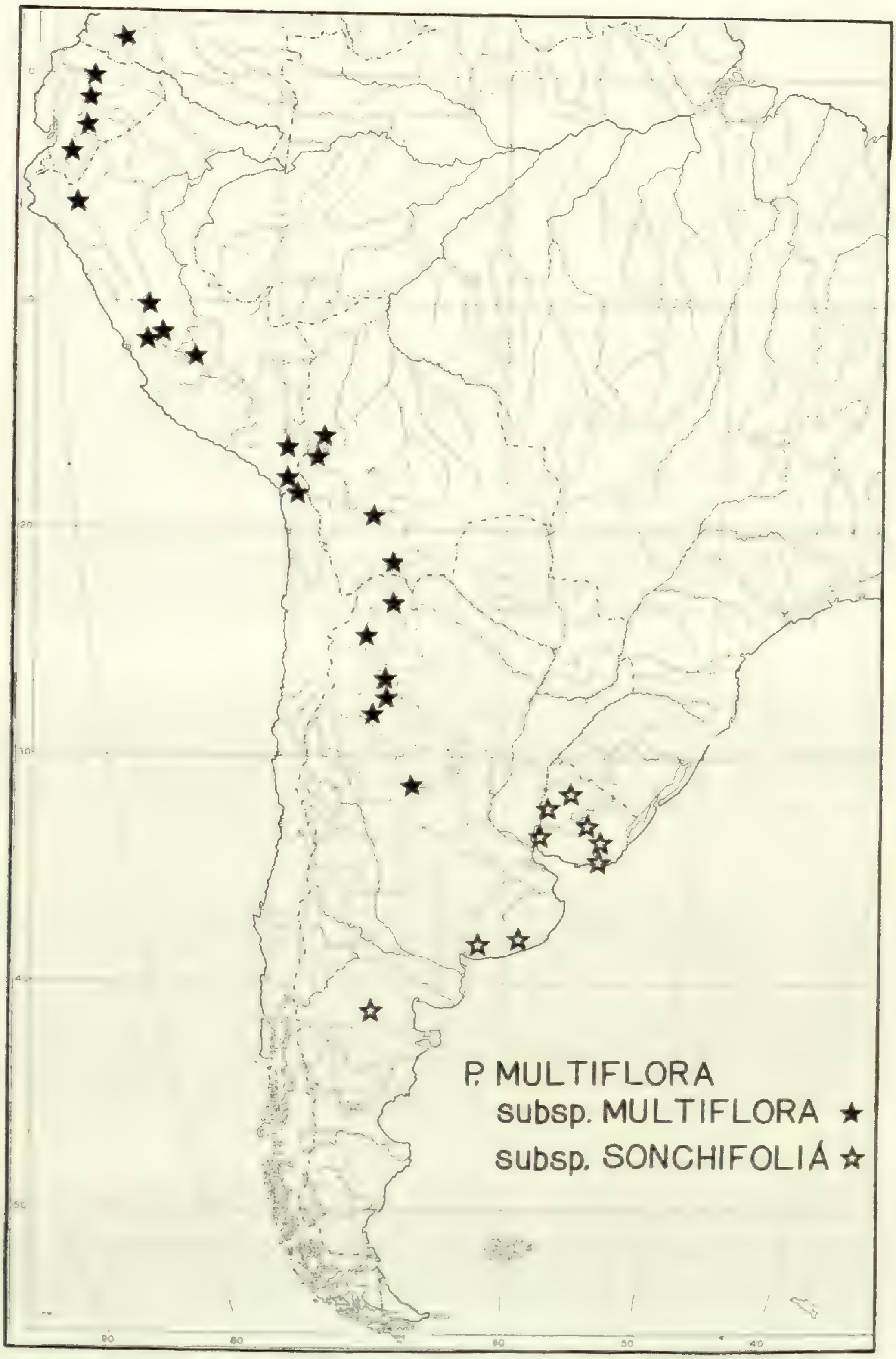


FIG. 18. Distribution of *Perezia multiflora*. In this, and all the subsequent distribution maps, symbols may represent one or several collections made at that locality. If two localities are very close together, they are indicated by only one symbol.

by the run-off waters during the rainy season. Another factor which has been influential in allowing the species to maintain its range is the prickly nature of the plants which discourages browsing by sheep and cattle. This habit gives *P. multiflora* a definite selective advantage over many other species which are killed off by grazing animals.

It is possible that there has also been active distribution of the species by man. Bunches of the leaves of *Perezia multiflora* subsp. *multiflora* are sold in the markets of the altiplano of Perú and are used as a remedy (in tea) for altitude sickness and general stomach trouble.

There is little difficulty in separating *Perezia multiflora* from the other species of the section because it is so distinctive and, except for some minor variation, exceedingly constant morphologically. The small populations in the Pampa de Achala show some morphological differences from the disjunct Andean populations. The Achala populations were considered to be a subspecies of *P. multiflora* by Kuntze because they have more open branching and fewer capitula. The florets of the Pampa de Achala populations also seem to be much brighter blue than those in the Cordillera. However, when a large series of specimens from the Andes is examined, enough variation is evident to warrant the inclusion of plants from Achala into *P. multiflora* subsp. *multiflora*.

Chromosome counts have been made for several populations of *Perezia multiflora* subsp. *multiflora*. Two counts were made from the main Cordillera (Ecuador and Perú) and one count from the Pampa de Achala population (Table 5). A haploid number of 8 was found in all cases.

1(b). Perezia multiflora subsp. sonchifolia (Baker) Vuilleumier comb. nov.

Perezia sonchifolia Baker in Martius, Fl. Brazil, 6(3):380. 1884. Type: URUGUAY. Canelones: Montevideo, *King 48* (K).

Perezia sonchifolia Baker var. *tandilensis* O. Kuntze, Rev. Gen. 3(2):167. 1898. Type: ARGENTINA, Buenos Aires: Ṭandil, XI–1892, *Kuntze s.n.* (US, Isotype LP).

Perezia aletes Macbride, Rhodora **20**:151. 1918. Type: UNITED STATES. Massachusetts: North Worcester, 9–IV–1918, *Horr s.n.* (GH).

Plants fairly small averaging 27 cm in height. Basal leaves absent at flowering time or generally shorter than 6 cm. Heads in an open inflorescence

resembling a flat topped panicle; usually about three capitula per flowering stem. Florets always white with the inner two petals and half of the corolla tube yellow. Ligules about 5 mm long.

Distribution: southern Uruguay, northeastern Argentina, and Río Negro, Argentina (Fig. 18).

Representative specimens: ARGENTINA. Buenos Aires: Boca de la Sierra, *Alboff s.n.* (LP); Tandil, XI–1892, *Kuntze s.n.* (LP, US), Sierra de Tandil, Conien, 24–X–1962, *Leal 22300* (LP). Río Negro: vicinity of General Roca, 250–360 m, IX–II–1914–1915, *Fisher 134* (GH, NY, US). BRAZIL. Santa Catarina: Serro do Oratorio in Araucarienwald, I–1889, *Ule s.n.* (HBG). URUGUAY. Tacuarembo: Arequita Minas, 300 m, XI, *Herter 486* (F, G, GH); Valle Eden, 200 m, 28–IX–1928, *Herter 486A* (GH). Río Negro: Paysandii, zwischen Tres Arboles und Paso de los Torros, X, *Herter 5078* (G); Tres Arboles, 4–X–1939, *Rosengurt B–3012* (NY). Canelones: Montevideo, *Arecharaleta s.n.* (LP). Maldonado: 11–X–1932, *Osten 22645* (GH); Banda oriental del Uruguay, 1816–1821, *Catal 2002* (P); Cerro de las Animas, *Chebataroff 2163* (LP). Durazno: 16–XI–1900, *Osten 4363* (G). Sierra de Tolis, XI–1892, *no collector* (NY).

Although *Perezia sonchifolia* has previously been considered to be distinct from *P. multiflora*, the trend of morphological variation present from west to east across central South America indicates that the *P. sonchifolia* populations are merely the ends of what was once a more "continuous" distribution of *P. multiflora* across the continent. These populations are considered here as a subspecies of *P. multiflora* rather than as a separate species. Going from west to east across the range of *P. multiflora* subsp. *multiflora*, there is a decrease in the size of the plants, the amount of spininess, and the number of heads per flowering stem. Correspondingly, there is a slight increase in the size of the individual capitula. The populations of *P. multiflora* subsp. *sonchifolia* in southern Uruguay are simply more extreme in all of these characters than the easternmost populations of *P. multiflora* subsp. *multiflora*.

There is a great difference in the altitude at which the two subspecies grow. *Perezia multiflora* subsp. *multiflora* grows at high elevations, subsp. *sonchifolia* is a lowland subspecies (Fig. 18). There is also one report of *P. multiflora* subsp. *sonchifolia* growing in an *Araucaria* woodland.

In conjunction with the difference in altitude at which the two subspecies grow, it is interesting to note that there is a statistically significant negative correlation in *Perezia multiflora* subsp. *multiflora* between (1) altitude and the width of the head, and, (2) altitude and the length of the ligule. *P. multiflora* subsp. *sonchifolia* is found at lower elevations than any plant of *P.*

multiflora subsp. *multiflora* and has broader heads and longer ligules than specimens of *P. multiflora* subsp. *multiflora*.

The only species to which *Perezia multiflora* subsp. *sonchifolia* is similar is *P. squarrosa* (especially subsp. *squarrosa*). The two are sympatric, however, in Uruguay, and can be distinguished easily on the basis of the basal leaves and the involucral bracts. The basal leaves of *P. squarrosa* subsp. *squarrosa* are present when the plant is flowering and are very spiny along the margins. Plants of *P. multiflora* subsp. *sonchifolia* have usually lost their basal leaves by flowering time or have a few curled leaves with rounded segments. The involucral bracts of *P. multiflora* subsp. *sonchifolia* are not spiny as they are in *P. squarrosa* subsp. *squarrosa*.

2. Perezia squarrosa (Vahl) Less.

Robust rosette plants 19–82 cm tall with a deep taproot. Flowering stems terete in cross section, slightly striated, bearing 7–20 stem leaves. Stem leaves linear-lanceolate, acute, sometimes divided into fleshy segments each of which is terminated by a sharp white spine, occasionally merely dentate and spiny; surface with glandular punctate dots and infrequently with a few scattered glandular trichomes. Basal leaves usually numerous, linear-lanceolate to broadly lanceolate in outline, mucronate, edges deeply divided into fleshy segments each terminated with a white spine, or shallowly dentate with dentate segments; attenuate at the base, 5–34 mm wide, 4–27 cm long; surface with scattered glandular trichomes and sometimes with a few very long (to 5 mm) multicellular glandular trichomes. Inflorescence a panicle of 4–70 heads. Individual capitula campanulate, 1–2.5 cm wide and 8–10 mm long; upright. Involucre hemispherical, 6–20 mm wide, 7–15 mm long, composed of 3–4 rows of bracts. Outer bracts oblong to ovate, or infrequently lanceolate, mucronate, spiny at the base; 1–4 mm wide, 4–11 mm long, with glandular trichomes on the surface and usually slightly scarious at the base. Inner bracts lanceolate to oblong, mucronate, entire, 1–3 mm wide, 6–18 mm long, glandular trichomes sometimes present at the apex; scarious at the base and along the margins. Pappus setose, 6–17 mm long, blond or red in color. Florets white, blue, violet, or magenta; outer florets 9–15 mm long with ligules 1–7 mm long; ligules frequently with glandular trichomes on the under surface; 10–31 florets per head. Immature achenes 2–3 mm long, covered with long silky double hairs over glandular trichomes. Mature achenes to 5 mm long, dark brown, with double hairs much more widely spaced than on the ovaries. Receptacles with tufts of long silky trichomes.

Distribution: southeastern Paraguay; Brazil in the provinces from Rio de Janeiro south; Uruguay along the southern border to the Atlantic Ocean (Fig. 22–1). Flowering from October to January.

KEY TO THE SUBSPECIES

Basal leaves with dense even white spines along the margin, heads broadly campanulate ..... 2a. *P. squarrosa* subsp. *squarrosa*.

Basal leaves with even teeth without spines, heads narrowly campanulate ..... 2b. *P. squarrosa* subsp. *cubaetensis*.

2(a). Perezia squarrosa (Vahl) Less. subsp. squarrosa

Perdicium squarrosum Vahl, Skriv. Nat. Selsk. Kiøb. **1**:11. Tab. 6, 1790. Type: URUGUAY. Canelones: sommet du Morne de Montevideo, 1767, *Commerson s.n.* (C, Isotype P).

Perezia squarrosa (Vahl) Lessing, Linnaea **5**:15. 1830.

Homoianthus squarrosus (Vahl) de Candolle, Prodr. **7**:64. 1838.

Homoianthus ambiguus Cassini, Opus. Phytol. **2**:167. 1826. An illegitimate name because it was superfluous when published. Cassini cited *Perdicium spuarrosum* Vahl in synonymy.

Plants robust, upright. Basal leaves with dense even white spines along the border. Inflorescence of heads corymbose. Individual capitula broadly campanulate. Outer bracts terminated by a white spine. Florets blue.

Distribution: southern Paraguay, Uruguay along the Uruguay River and the Atlantic coast (Fig. 22–1). Flowering from November to December.

Representative specimens: PARAGUAY. Paraguari: Ybytimi, 9–X–1952, *Montes 12951* (LP). Guaira: Iturbe, 20–IX–1952, *Montes 12919* (LP). URUGUAY. Canelones: sommet du Morne de Montevideo, IX–1767, *Commerson 93* (P), XI–1864, *Fruchard 55* (P). Maldonado: Cerro de las Animas, *Chebataroff 3006* (LP); Cerro Blanco, oeste del Cerro de las Animas, 400 m, *Chebataroff 3008* (LP); east bank of Rio Uruguay, 1816, *Catal 2082* (LP).

2(b). Perezia squarrosa (Vahl) Less. subsp. cubaetensis (Less.) Vuilleumier Comb. nov.

Perezia cubaetensis Lessing, Linnaea **5**:16. 1830. Type: BRAZIL. Santa Catarina: Cerro de Cubatao, *Sello 3840* (Type destroyed at Berlin, Isotype P).

Homoianthus cubaetensis (Less.) de Candolle, Prodr. **7**:64. 1838.

Perezia laevis Less. Linnaea **5**:18. Tab. 1, Fig. 22 f&g. 1830. Type: BRAZIL, without locality, *Sello s.n.* (P).

Homoianthus laevis (Less.) DC. Prodr. **7**:64. 1838.

Plants tall, fairly lax. Basal leaves with even soft teeth. Inflorescence of heads a large panicle. Individual capitula narrowly campanulate. Outer bracts lanceolate, acute. Florets blue, violet or reddish in color.

Chromosome number: $2n=8$.

Distribution: southeastern Brazil. Flowering from October to January (Fig. 22–1).

Representative specimens: BRAZIL. Rio de Janeiro: Itatiaia, Campo do Silverio, 23–I–1873, *Glaziou GS80* (P). São Paulo: Capital, 18–X–1893, *Edwall 17004* (NY); Butantair, 12–X–1917 *Hoehne 681* (US); Rua Consolação, *Hoehne* (US). Santa Catarina: Matos Costa, 1200 m, 9–XII–1962, *Klein 3584* (LP), 1200 m, 27–X–1962, *Reitz & Klein 13717* (LP); Serra do Boa Vista, São Jose, 1000 m, 13–X–1960, *Reitz & Klein 10164* (LP); Campo Alegre, 1000 m, 17–X–1957, *Reitz & Klein 5158* (US), campo and pinheiral, 4 km S. of Campo Alegre on the road to Jaragua do Sur, 900–1000 m, 6–XI–1956, *Smith & Klein 7323* (NY, US); Serro do Oratorio, Bom

Jardim, São Joaquim, 1400 m, 23–X–1958, *Reitz & Klein 7462* (LP); Serra do Boa Vista, São Jose, 24–X–1957, *Reitz & Klein 5361* (LP); Marombas Curitibanos, 900 m, 29–X–1962, *Reitz & Klein 13897* (LP); Cacador, Fazenda Carneiro, northeast of Cacador, 950–1100 m, 21–XII–1956, *Smith & Reitz 8995* (US). Parana: Pinhaes in ruderatis, 835 m, 16–IX–1914, *Dusén 946a* (GH); Serra do Mar, Desiro Ypiranga ad viam ferream, 700 m, 31–XI–1914, *Dusén 15782* (GH); Curitiba, in campo graminoso, 7–X–1908, *Dusén 6805* (US), Capa do Imbuia–Curitiba, II–1964, *Dombrowski 1659* (A); Vallinhos in "capocira," 10–XI–1910, *Dusén 10764* (NY). Rio Grande do Sul, 31–X–1958, *Richter 4 B7828* (F); Aparados da Serra, 1300 m, 24–X–1961, *Pabst 6296* (LP). Brazil without locality, *Sello s.n.* (P). *Sello 3840* (P).

Although data are scarce for *Perezia squarrosa*, it appears that the species is usually found in humid places, in southern Brazil, Paraguay and Uruguay (Fig. 22–1), at low elevations or even at sea level.

The populations which are included here in one taxon were formerly considered to constitute three distinct species: *Perezia squarrosa* from Uruguay; *P. cubaetensis* from southeastern Brazil; and *P. laevis* from eastern Paraguay. Collections from all of these areas are poor and consequently treatment of the taxa has been conservative. I have now seen collections from southern Brazil (Río Grande do Sul and Paraná) which show many intermediate characteristics between those found in plants from Brazil and those from Uruguay. Correlations of morphological characters with latitude and longitude indicate that there is a trend toward the northeast (toward Cubatão, Brazil from Montevideo, Uruguay) for plants to become taller, more branched, and to have smaller capitula and larger leaves. In other words, although the Brazilian and the Uruguayan populations are disjunct, they approach one another in morphology at the closest part of their respective ranges. In view of the allopatry of the two sets of populations, and the discontinuity in morphology, I have treated them as subspecies.

Although Baker (1884) placed *Perezia laevis* in the synonymy of *P. multiflora*, it seems to belong more naturally with *P. squarrosa* subsp. *cubaetensis* because both share the features of small head size and lax flowering stems.

In achene pubescence, foliar trichomes, and the reduced number of involucral bracts, *Perezia squarrosa* is very similar to *P. multiflora*. Although the *P. multiflora* species group is a very tightly knit assemblage, there seems to be a closer relationship of

P. squarrosa with *P. multiflora* than of either of these two species with *P. kingii*. *Perezia squarrosa* subspecies *squarrosa* differs from *P. multiflora* by having larger heads, fewer involucral bracts, and narrower leaves. The subspecies *cubaetensis* differs from *P. multiflora* in its less spiny basal leaves, smaller capitula, and more open branching of the flowering stalk.

3. Perezia kingii Baker

Perezia kingii Baker, Mart. Fl. Brazil. 6(3):380. 1884. Type: URUGUAY. Concepción: Puerto de Salamanca, X–1875, *Lorentz s.n.* (Type destroyed at Berlin, Isotype GH).

Very tall, weedy appearing rosette plant 18–91 cm tall with a long thick taproot. Stem terete in cross section, covered with a dense layer of glandular trichomes. Stem leaves 10–numerous, scattered up the stem, lyrate in outline, acute, dentate with each of the segments ending in a small spine, clasping; up to 3 mm wide and 15 mm long, surface with multicellular glandular trichomes. Basal leaves sometimes lacking, sometimes in a small flat rosette; lanceolate to lyrate in outline, acute, exceedingly lacerated with the deep teeth once or twice more dentate; attenuate at the base; 9–25 mm wide and 2.5–10 cm long, surface with scattered glandular trichomes. Inflorescence a loose panicle of 6 to many small heads. Capitula campanulate, 9–14 mm wide, 6–10 mm long, sometimes nodding. Involucre hemispherical, 9–13 mm wide, 6–9 mm long, composed of 2 rows of bracts. Outer bracts lanceolate, mucronate, stiff and shiny, with small white spines near the base; 1–2 mm wide, 5–9 mm long, surface with grandular trichomes, non-scarious. Inner bracts lanceolate, mucronate, 2–3 mm wide, 5–8 mm long, surface with glandular trichomes, especially near the apex; slightly scarious to almost two-thirds scarious along the edges. Pappus setose, white, 4–5 mm long. Florets inconspicuous, white, and only slightly protruding from the involucre, outer florets 6–8 mm long with ligules 1–2 mm long; about 10–14 florets per head. Immature achenes 2–3 mm long, densely covered with silky blond or red double hairs. Mature achenes about 2 mm long. Receptacle covered with tufts of long blond or reddish trichomes around the point of ovary attachment.

Distribution: along the western Argentina-Uruguay border at sea level (Fig. 22–1). Flowering from September to December.

Representative specimens: ARGENTINA. Entre Ríos: Victoria, Victoria, 1–XI–1946, *Meyer 10179* (LIL). Corrientes: X–1820, *Bonpland 352* (P). Río Colorado, IX–1904, *Dinelli s.n.* (BAB). URUGUAY. Banda oriental del Uruguay, 1816–1821, *Catal 2312* (P). Florida: Cerro Colorado, Arroyo Timote, 15–X–1942, *Gallinal, Aragone, Bergalli, Campal, Rosengurtt PE 5–334* (GH). Concepción del Uruguay, Puerto de Salamanca, X–1875, *Lorentz s.n.* (GH).

Apparently, *Perezia kingii* is a fairly rare species. Collections are few, and it has not been recorded more than four or five times in this century. The collectors' notes indicate that the species grows in sandy localities. The prevalence of collections from the

banks of the Uruguay River indicate that it is a riverine species. Because of its limited distribution (Fig. 22–1) and the scanty herbarium material, it is impossible to say whether *P. kingii* exhibits any geographical variation in morphological characters.

In my opinion, there is no doubt that *Perezia kingii* is closely related to, but distinct from, *P. squarrosa* and *P. multiflora*. Along the banks of the Uruguay River it is sympatric with *P. multiflora* subsp. *sonchifolia* and *P. squarrosa* subsp. *squarrosa*. I have seen no specimens suggesting that hybridization has occurred. *Perezia kingii* is closely related to the other members of the *P. multiflora* species group as shown by the same type of dense copper or blond double trichomes on the achenes, the pubescence on the receptacle, the reduced number of rows of outer bracts, and the small pollen size.

However, the very small capitula size is a unique character of *Perezia kingii* allowing it to be readily distinguished from the other members of the *P. multiflora* species group. The many heads, loose branching, and the pure white pappus are also unique to *P. kingii*. These characters are suggestive of some species of *Leucheria* and *Trixis*.

4. Perezia prenanthoides Less.

Perezia prenanthoides Lessing, Synop. Comp. 409. 1832. Type: CHILE. Bío Bío: Andes de Antuco, Valle de Quilai, II–1830, *Poeppig 923* (P. Isotypes F, G, NY).

Perezia brachylepis Philippi, Anal. Univ. Chile **87**:299. 1894. Type: CHILE. Cautín: Boquete de Trancura, II–1887, *O. Philippi 2251* (SGO).

Showy, tall plants 27–84 cm tall with large basal leaves and leafy stems. Stems terete, variable in pubescence, but usually with increased amounts of glandular trichomes near the inflorescence; sometimes red streaked. Stem leaves about four up to the point of the first branching, numerous above; lower leaves lyrate, parted with the segments dentate, clasping, up to 2.5 cm wide and 7 cm long; decreasing in size until almost scale-like under the ultimate branchlets. Basal leaves lyrate or runcinate, parted with dentate segments, acute, attenuate at the base, 4–13 cm wide, 12–40 cm long, glabrous to slightly pubescent with the scattered glandular trichomes denser along the veins of the under surface of the leaf blade. Inflorescence a flat topped cyme of 3–25 heads; only one flowering stalk per rosette. Individual capitula campanulate, 1.8–2.4 cm wide, 1.2–3 cm long; upright. Involucre hemispherical, 6–20 mm wide, 6–18 mm long; composed of 3 or 4 rows of bracts. Outer bracts ovate to broadly lanceolate, acute, 1–3 mm wide and 4–6 mm long, sometimes with scattered glandular trichomes on the surface; frequently dark red on the upper portions; non-scarious. Inner bracts lanceolate, acute, 1–2 mm wide, 7–10 mm long; reddish at the tip in many specimens; non-scarious. Pappus setose, fairly abundant, usually

deep red in color, 10–16 mm long. Florets rose, pink, or maroon; outer florets 1.5–3.3 cm long with ligules 4–15 mm long; about 31 per head. Ovaries and achenes with scattered glandular trichomes; sometimes with a few scattered double hairs at the top. Receptacle convex with a few scattered silky trichomes.

Distribution: from Malleco in Chile south to Llanquihue and in Argentina in the provinces of Neuquén and Río Negro (Fig. 25–4). Altitudinally between 1200 and 1550 m. Flowering from January to March. See PLATE 1–4.

Representative specimens: ARGENTINA. Neuquén: Lago Lolog, 3000 ft, *Comber 1064* (K). Río Negro: Parque Nacional Nahuel Huapi, near Laguna los Clavos, 19–III–1949, *Lourteig 267* (P), Cerro Otto, 8–II–1965, *Vuilleumier 185* (GH), 9–II–1965, *Vuilleumier 191* (GH). CHILE. Bío Bío: Andes de Antuco, Valle de Quitai, *Poeppig 923* (P). Malleco: Cordillera de Nahuelbuta, Fundo Solano, Los Alpes, 2000 m, 13–I–1958, *Eyerdam 10163* (F, US); before the city of Lonquimay, 31–III–1965, *Vuilleumier 221* (GH); Volcán de Tolguaca, 24–II–1925, *Pennell 12790* (GH); Cordillera Las Raices, 2–III–1939, *Burkart 9574* (SI). Cautín: Volcán Llaima, 1200 m, II–1927, *Werdermann 1230* (F, GH, HBG, NY, SI, US); Temuco, Refugio, 3–II–1961, *Ricardi & Matthei 5318/122* (CONC); Boquete de Trancura, II–1887, *O. Philippi s.n.* (SGO). Llanquihue: Cerro Vichadero, Casa Pangue, 14–I–1953, *Pfister s.n.* (CONC).

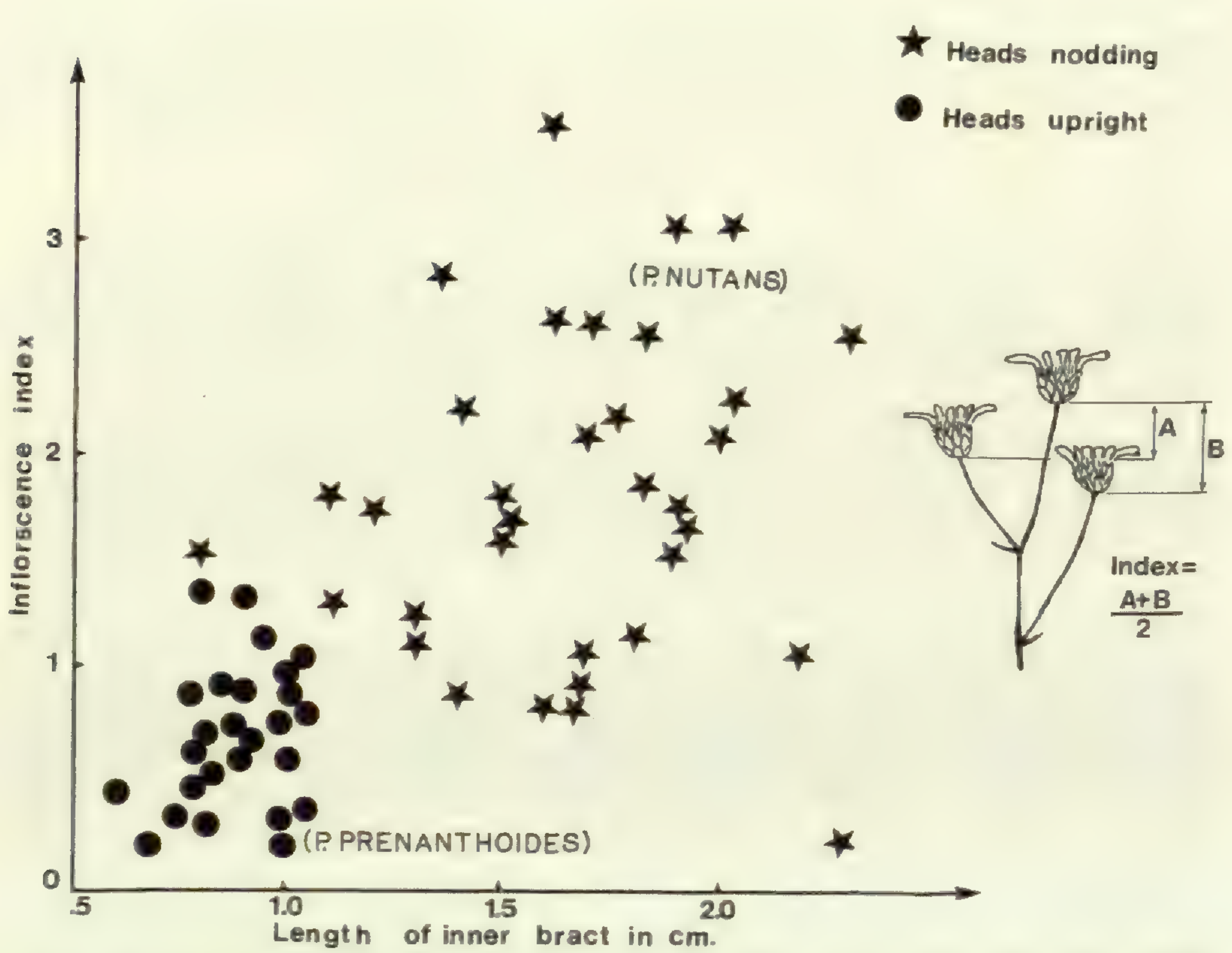


FIG. 19. Graph of inflorescence *vs.* inner bract length of *Perezia prenanthoides* and *P. nutans* showing the neat separation of these two very closely related species of the *P. prenanthoides* species group. Each symbol represents one specimen.

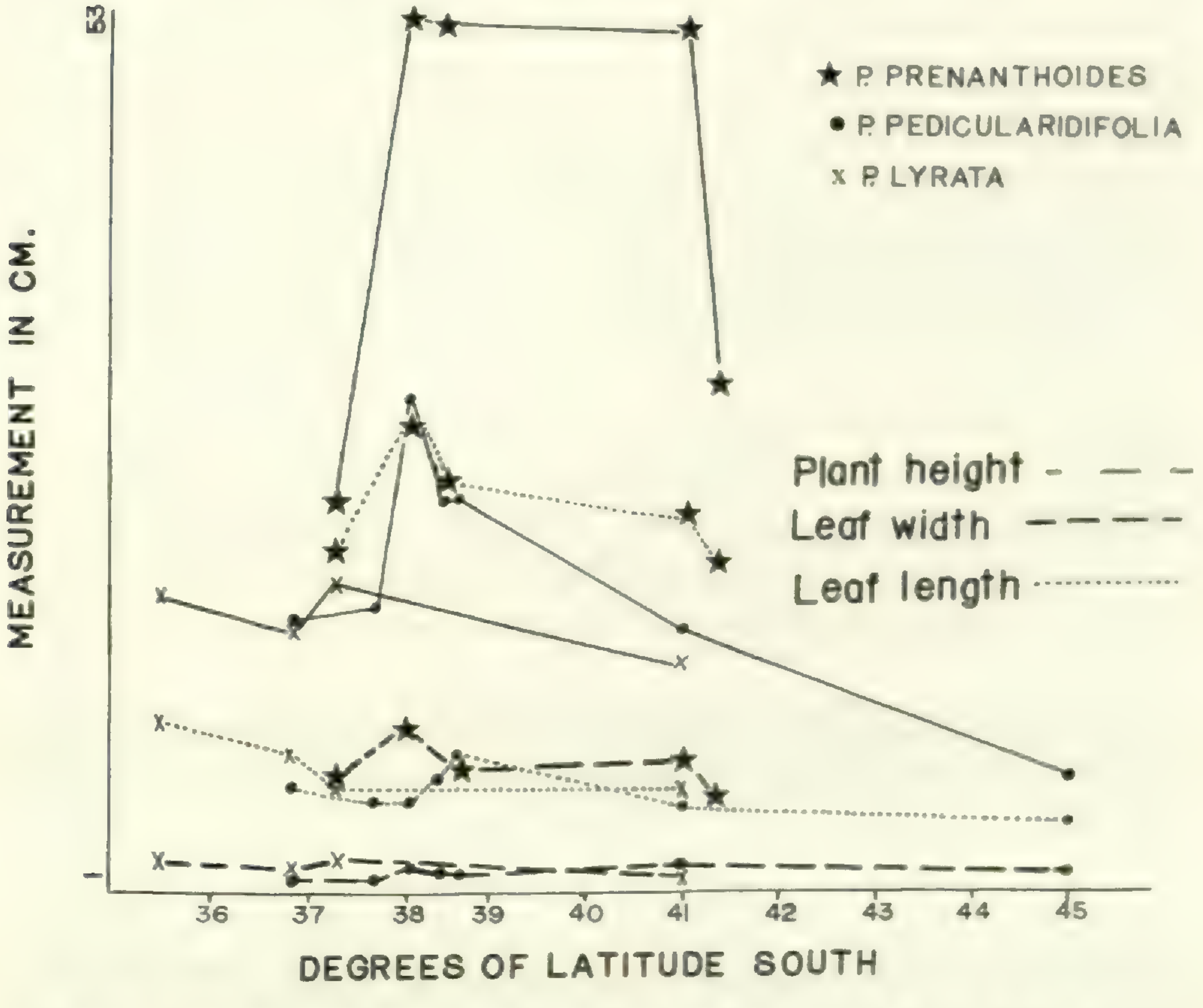


FIG. 20. Graph of plant height, leaf length, and leaf width *vs.* latitude of three species of *Perezia* inhabiting the *Nothofagus* forest of southern South America. The graph shows that the largest plants of these three species are found in populations between 37° and 42°S. where the forest is most lush. To the north, the forest diminishes due to increased aridity, and to the south the increased cold becomes an inhibitory factor.

Throughout the *Nothofagus* forest in the lake region of Argentina and Chile, *Perezia prenanthoides* is a conspicuous plant (PLATE 1–4) in the early summer. Its showy clusters of magenta heads are visible in patches in the higher elevations of the forest along with *Chusquea* (a bamboo) and, in several places, with the smaller, blue-flowered *P. pedicularidifolia*.

Reiche distinguished the two species, *Perezia prenanthoides* and *P. brachylepis* (treated here as one taxon) on the basis of the width of the outer bract and the length of the inner bracts relative to the length of the florets. There is a discernible trend for plants to become gradually smaller (in all dimensions) as one goes south in the range (Fig. 20). It is noteworthy that the type specimens of *P. prenanthoides* and the synonym *P. brachylepis* are from the extreme ends of the range and were described at a time when intermediate specimens might not have been available.

The two species, *Perezia prenanthoides* and *P. nutans* form an isolated species group within the South American *Perezia*. Their similarity in habit, morphology, and ecology, however, suggests that they are only recently differentiated from one another. That they have attained specific rank is attested to by a large amount of sympatry in their ranges without apparent hybridization and by several distinctive characters. Figure 19 graphically shows that the two form well defined taxa on the basis of involucral bract size and the type of branching of the flowering stems. *Perezia prenanthoides* has a compact branching habit which produced an arrangement of heads similar to a cyme. The individual heads are small, upright, and hemispherical. In contrast, *P. nutans* has a loose, paniculate arrangement of heads and nodding, turbinate capitula.

Because of its large showy inflorescence of pink flowered heads (PLATE 1–4), *Perezia prenanthoides* is almost impossible to confuse with any other speices of *Perezia* except *P. nutans*. The only species to which it is vaguely similar are those of the *P. multiflora* group. Species of this assemblage, however, have spiny foliage and achenes densely covered with copper colored double trichomes whereas both *P. prenanthoides* and *P. nutans* have soft leaves and achenes with glandular trichomes.

5. PEREZIA NUTANS Less.

Perezia nutans Lessing, Synop. Comp. 409. 1832. Type: CHILE. Antuco, Meseta de Antuco, I–1830, *Poeppig 896* (P, Isotypes GH, NY).

Perezia gayana de Candolle, Prodr. 7:63. 1838. Sel. Icon. 4:tab. 94. 1839. Type: CHILE. Colchagua, *Gay 313* (P, Isotype G).

Perezia perfoliata Remy in Gay, Fl. Chile 3:415. 1849. Type: CHILE. Colchagua, Cordillera de San Fernando, *Gay s.n.* (P, Isotypes F, GH, NY, US).

Tall attractive plants with inflorescences of nodding heads of sweet smelling flowers. Plants 24–84 cm tall. Stems terete, frequently slightly striated, sometimes with a reddish tinge and usually with some glandular trichomes, especially near the inflorescence. Stem leaves 2–5 to the point of first branching and numerous above; the lower stem leaves lyrate to runcinate, acute, and divided into large dentate segments; the upper stem leaves reduced to bracteoles. Basal leaves lyrate, obtuse to acute, with large teeth secondarily dentate, attenuate at the base; 2.5–10 cm wide, 8–31 cm long; a few scattered glandular trichomes usually present on the surface and along the veins. Inflorescence a diffuse panicle of 2–31 nodding capitula. Individual capitula turbinate, 1.9–4.2 cm wide and 1.7–3 cm long. Involucre turbinate, 1.5–3.7 cm wide, 1.5–2.2 cm long; composed of 3–5 rows of bracts. Outer bracts ovate or lanceolate, acute, entire, 1–3 mm wide, 4–16

mm long; usually green but sometimes with a slight reddish tinge; non scarious. Inner bracts lanceolate to linear-lanceolate, acute, 1–5 mm wide, 8–22 mm long, green and slightly scarious along the edges. Pappus setose. blond or reddish in color, 8–18 mm long. Corollas magenta, violet, lavender, or purple; outer florets 1.7–2.6 cm long with ligules 6–12 mm; about 25 flowers per head. Ovaries and achenes with scattered glandular trichomes of variable density. Mature achenes up to 4 mm long. Receptacle glabrous in specimens seen.

Distribution: Valparaiso in central Chile to Malleco, eastward in Argentina in the province of Neuquén (Fig. 25–4). Altitudinal range from 1200–2500 m. Flowering from November to March.

Representative specimens: ARGENTINA. Neuquén: Dpto. Minas, 36 43'S, 71°37'W, 1–II–1964, *Boelcke, Correa & Bacigalupo 11460* (LP) 36 50'S 71°04'W, 1300 m, 15–I–1964, *Ibid 10885* (LP). CHILE. Valparaiso: Cerro Campana, 1200 m, 17–I–1939, *Morrison & Wagenknecht 17142* (GH), SW slope, 1500 m, 19–I–1936, *West 5182* (GH). Santiago: Valle del Río Volcán, La Engerda, 2600 m, III–1933, *Grandjot s.n.* (CONC, HBG); mountains above Río Colorado, 3800 ft, 21–I–1902, *Hastings 421* (NY); Valle del Yeso, entre Lo Valdés y las Yeseras, 2450 m, 11–II–1963, *Ricardi, Marticorena & Matthei 829* (CONC), Laguna Negra, 10000 ft, 6–II–1902, *Hastings 490* (NY, US). Colchagua: Cordillera de San Fernando, *Gay s.n.* (F, GH, P, US); Baños del Flaco, 19–XII–1938, *Moreau 23469* (LP). Nuble: Termas de Chillán, 1800 m, *Cabrera 3629* (LP), Cuesto de Pirigallo, 20–II–1958, *Codero s.n.* (CONC), Lecheria, 11–II–1960, *Pfister s.n.* (CONC), rocky cliffs, 1800–1900 m, *Pennell 12380* (F, GH, NY, US), 1800–1900 m, 31–III–1965, *Vuilleumier 223* (GH). Bío Bío: Cordillera de Bío Bío, Cerro del Padre, 11–II–1939, *Barros 2632* (SI); south of Laguna de la Laja, las Cuevas, 26–XI–1941, *Behn s.n.* (CONC); Antuco, Huingan, 15–I–1941, *Junge 2429* (CONC, LP), I–1830, *Poeppig 896* (G, NY, P). Malleco: Lonquimay, Laguna San Pedro, 3–II–1953, *Pinto s.n.* (CONC).

Like *Perezia prenanthoides, P. nutans* is a woodland species inhabiting the upper reaches of the *Nothofagus* forest (Fig. 25–4). In the northern part of its range, Valparaiso and Santiago, it inhabits more open areas than further south. Old illustrations indicate that, until very recently, there was more forest in the upper valleys of rivers in the Santiago region than today. Consequently, the distribution of *P. nutans* has probably been recently constricted.

The populations which I feel should be included in *Perezia nutans* were formerly considered to be three species: *P. nutans, P. perfoliata,* and *P. gayana*. Reiche maintained all three species in his *Flora de Chile* and distinguished the species on the basis of the density of the stem pubescence and by the "shape" of the stem leaves.

The amount of pubescence is extremely variable in almost all species of *Perezia* and is not a character of specific value. The "shape" difference utilized by Reiche is actually a difference in

leaf width rather than an actual shape difference. The size and broadness of the leaves of *Perezia nutans* appears to vary with the amount of sunlight, exposure, and moisture. There is an increase in leaf size from north to south as the rainfall and forest cover increases.

Although *Perezia nutans* is very similar morphologically to *P. prenanthoides*, it can be separated on the basis of the inflorescence type and the outline and direction of the heads. Figure 19 shows that a combination of these two characters clearly separates the two taxa involved.

6. Perezia pungens (H. & B.) Less.

Chaetanthera pungens Humboldt & Bonpland, Pl. Aequin. **2**:146. Planche 127. 1809. Type: ECUADOR. Pichincha: Mt. Pichincha near Quito, *without collector* (P, in the Humboldt Herbarium).

Homanthis pungens (H. & B.) Humboldt, Bonpland & Knuth, Nov. Gen. Sp. Plant. 4:14 (quarto edition). 1820.

Homoeanthus pungens (H. & B.) Sprengel, Sys. Veg. 3:503. 1826.

Perezia pungens (H. & B.) Lessing, Linnaea **5**:20. 1830.

Clarionia pungens (H. & B.) D. Don, Phil. Mag. **11**:388. 1832.

Drozia dicephala Cassini, Opus. Phytol. **2**:171. 1826. From the description, Cassini's specimen belongs in synonymy with *Perezia pungens*. However, Cassini cited no type and I can find no specimen labeled with this name.

Homoianthus scaber Bentham, Pl. Hart. 136. 1844. Type: in the mountains of Chuquiribamba (which I assume is in Perú or Bolivia). On page 353 of the same work (1857), Bentham stated in the errata that the species *H. scaber* was synonymous with *Perezia pungens*. I have not seen Bentham's type.

Clarionea macrocephala Schultz-Bipontinus in Lechler, Berb. Amer. Austr. 57. 1857. This name was a *nomen nudum* and thus not validly published. Tovar's transferral of the name to *Perezia* in 1955 is also, therefore, not valid.

Leucheria fasciata Klatt, Engl. Bot. Jahrb. 8:51. 1886. Type: ECUADOR. Pichincha: Mt. Pichincha, 4000 m, 4–I–1881, *Lehman 386* (GH).

Perezia elongata O. Kuntze, Rev. Gen. 3(2):166. 1898. Type: BOLIVIA. Cochabamba: on the road between Cochabamba and Río Juntas on the east slope of the Andes, 3600 m, 1896. *Kuntze s.n.* (NY).

Perezia stubelii Hieronymus, Engl. Bot. Jahrb. **21**:372. 1896. Type: PERU. Cajamarca: between Pacamayo and Mayobamba, 3650 m, *Stubel 34* (types of the Berlin Herbarium, destroyed during World War II, photo (GH).

Perezia pungens (H. & B.) Less. var *cernua* Rusby, Mem. Torrey Bot. Club 6:70. 1896. Type: BOLIVIA. Cochabamba: Mt. Tunari, 1891, *Bang 1049* (NY, Isotypes GH, US).

Perezia weberbaueri Hieron. ex Domke, Notizbl. Bot. Gart. Berlin **13**:249. 1936. Type: PERU. Puno: Sandia, above Cuyocuyo, 3800 m, 3–V–1902, *Weberbauer 933* (G).

Perezia aracensis Koster, Blumea **5**:678. Figure 7 a-d. 1945. Type: BOLIVIA. Araca, 4400m, XII–1910, *Bock 2480 b* (type not seen).

Perezia obtusisquama Koster, Blumea **5**:680. Figure 7 k-o. 1945. Type: BOLIVIA. Cochabamba: alpine meadows above Tablas, V–1911, *Herzog 2163* (type not seen, Isotype LP).

Perezia fosbergii Tovar, Pub. Mus. Hist. Nat. Lima Bot. 8:22. Figure 9. 1955. Type: PERU. Cajamarca: Celendín, Las Lajas, northwest slopes of Cerro Alto, southeast of Cortagama (Chimuch), 35 km north-northeast of Celendín, 3500 m, 3–VI–1947, *Fosberg 28123* (USM, Isotype F).

Perezia conaicensis Tovar, Pub. Mus. Hist. Nat. Lima Bot. 8:31. Figure 14. 1955. Type: PERU. Huancavelica: Huancavelica, Conaica, Laria, 8 km southwest of Conaica, 3900–4000 m, 30–III–1952, *Tovar 903* (USM, Isotype GH).

Leafy, caulescent plants with a scanty basal rosette (except in the Cajamarca populations); plants 6–70 cm tall. Stem round in cross section, densely glandular, pubescent; often reddish in color. Stem leaves 1–65 scattered up the stem, lanceolate to elliptical, acute (obtuse in Cuzco, Perú and northern Bolivia), entire or dentate, clasping, often cordate at the base, very variable in size; surface with a variable amount of glandular trichomes. Basal leaves in a loose rosette (except in some plants in Cajamarca, Perú) or, rarely, shriveled at flowering time, lanceolate to elliptical, acute, usually with large uneven teeth, more rarely spiny or entire; petioled for about one-half the length of the leaf or clasping; 6–50 mm wide, 4.5–40 cm long; usually densely pubescent. Plants monocephalous or more rarely with up to 9 heads per flowering stem and up to 14 per rosette. Capitula campanulate, 1.5–5 cm wide, 1.2–3.6 cm long; upright or nodding. Involucre hemispherical or slightly turbinate, 1–3.5 cm wide, 1–2.6 cm long; composed of 3–7 rows of bracts. Outer bracts lanceolate, ovate, or slightly spathulate, acute, serrate or entire; 1–7 mm wide, 5–22 mm long; soft, bearing glandular trichomes; often with reddish streaks. Inner bracts lanceolate, acute, entire or slightly serrate at the apex; 1–5 mm wide, 1–2.5 cm long. Pappus setose, brown, 6–20 mm long. Florets white, blue, violet or pinkish; the inner two petals of the floret sometimes lighter in color than the ligule. Outer florets 1.3–3.5 cm long with ligules 5–20 mm long; from 10–68 florets per capitulum. Immature achenes 1–4 mm long, with a variable amount of glandular trichomes. Mature achenes to 4 mm in length, surface as in the ovaries. Receptacle glabrous.

Chromosome number: Pichincha, Ecuador, $n=12$.

Distribution: from southern Colombia through Ecuador, Perú and into northern or central Bolivia (Fig. 21). Apparently in wet, fairly tall puna grass. Altitudinal range from 2500–4600 m. Flowering from February to July. See PLATE 1–1.

Representative specimens: COLOMBIA. Pasto: 3200 m, *Triana 1511* (P). ECUADOR. Imbabura: Lake Cuicocha, 3300 m, 28–V–1939, *Pentland & Summers* 739 (F); northeast slope of Cayambe mountain, 14500 ft, 16–XII–1961, *Cazalet & Pennington 5780* (NY); slope of Cotachi peak, 4400 m, 31–V–1939, *Pentland & Summers 8021* (F); above Aparejos, selva Alegre, west of Otavalo, 11200 ft, 23–IV–1944, *Drew E–143* (US). Pichincha: 18–VIII–1964, *F. Vuilleumier 2* (GH). Napo-Pastaza: Antisana, Hacienda Antisana, 4100 m, 21–VII–1960, *Grubb, Lloyd, Pennington & Whitmore 574* (NY); near Los Llanganti between Aicilibi and Río Potero east of Roma Páramo, 3600 m, 31–IX–1959, *Barclay & Juajibioy 9203* (US); Cotopaxi, Cordillera Occidental Páramo de Apagua between Zumbagus and Pilalo, 3800 m, 18–19–VII–1959, *Barclay & Juajibioy s.n.* (US). Chimborazo: Hacienda Magna east of Chunchi, Páramo de Cacheaco, 3800 m, 27–VII–1959, *Barclay & Juajibioy 8284* (US). PERU. Cajamarca: Cumullca, 20–V–1965, *Vuil-*

leumier 251 (GH); Celendín, 3700 m, 6–X–1958, *Ferreyra 13277* (GH). Amazonas: Chachapoyas, upper slopes and summit of Cerro Campanario, 3600–3900 m, 3–VII–1962, *Wurdack 1560* (US). La Libertad: Patáz, entre Retamas y La Paccha, 3740 m, V, *Lopez & Sagastegui 3598* (LP). Ancash: encima de Huaráz entre Punta Caillán y Cajamarquilla, 4100–4200 m, V, *Ferreyra 14310* (GH); Cordillera Blanca, Quebrada Ulbe, 4400 m, *Raube & Hirsch 12082* (NY). Junín: Yauli, 13500 ft, *Macbride & Featherstone 925* (F). Cuzco: Calea, Pisac, 4000 m, II–1950, *Marin 1898* (F); Paucartambo, Acjanacu Pass, 9–V–1965, *Vuilleumier 250* (GH); Marachea hills of Escalerayoc, 3700–4200 m, 31–VII–1939, *Vargas 11180* (F); Pillahuata, VIII–1939, *Herrera 3335* (US); Chubamba, 3800 m, 4–III–1962, *Diaz 2034* (LP); Paso Tres Cruces, Cerro de Cusilluyoc, 3800–3900 m, 3–V–1925, *Pennell 13884* (F, GH, NY, US); Urubamba, lomas de Puyupata, 3000–3800 m, III–1942 *Vargas 2730* (LP). BOLIVIA. La Paz: La Fabulosa, 15000 ft, above the valley, *Brooke 6299* (BM); Larecja, Sorata, 3300–3800 m, *Mandon 25* (F, GH, K, NY, P). Cochabamba: plateau, Mt. Tunari, 1891, *Bang 1049* (GH, NY, US); Choro, Aparcita, 12400 ft, 3–II–1950, *Brooke 6100* (BM, F, NY); road to Chimore, 3000 m, IV–1939, *Cárdenas 765* (US); Chapare, 3100 m, 9–III–1929, *Steinbach 9562* (GH). Oruro: Espirito Santo, 1891, *Bang 1218* (G, GH, NY, US).

There is considerable variation in *Perezia pungens* from its northern limit in Colombia to its southernmost populations in Bolivia. The populations originally described as *Chaetanthera pungens* by Humboldt and Bonpland occur from Colombia through southern Ecuador, growing on volcanic peaks in tall, wet grass. Morphologically, although very variable, plants from these areas are large and have leafy flowering stems. The species has been described as being monocephalous, but there are now numerous specimens with polycephalous flowering stems from Pichincha, Ecuador and surrounding mountains. Plants with cemous capitula are frequently encountered in this area. The leaves, stems, bracts, and achenes of the Ecuador populations are almost without exception covered with glandular trichomes. Although the basal leaves are usually petioled, numerous examples can be found with clasping basal leaves.

Populations described as *Perezia stubelii* by Hieronymus are found on the moist, east facing slopes of mountain passes (jalcas) in the Department of Cajamarca, northern Perú. These plants supposedly differ from *P. pungens* because they have clasping basal leaves and strigose (double hairs) trichomes on the achenes. However, examples of *P. pungens* which are very similar to these plants can be found in Ecuador. Thus it appears that the "jalca" populations are merely isolated, and slightly different, forms of *P. pungens.*

Further east in Cajamarca is another species, known from only two specimens. These rather bizarre plants, described by Tovar as *Perezia fosbergii,* are much larger than any previously known specimens from this area. They are paniculately branched with numerous heads. Analyses of the pollen diameter and stomata size indicate that these plants are not polyploids. Since the description of *P. fosbergii,* other collections have been made still further east in the Department of Amazonas (Perú). One specimen I have seen *(Wurdack 1560)* is as large as those described as *P. fosbergii,* and has a rosette of clasping, evenly toothed leaves, but is monocephalous. The presence of these newly collected populations indicates that *P. fosbergii,* like *P. stubelii,* is referable to *P. pungens.*

Tovar described another species in 1955 from central Perú (Huancavelica) which he called *Perezia conaicensis.* When a large series of specimens of *P. pungens* is examined, it is evident that the type of this putative species falls completely within the range of variation of the former and I can therefore see no reason to maintain it as a species.

In the extreme south of Perú, on the wet passes in Cuzco, there are several populations (rapidly disappearing because of the spread of farming) which have long been known as *Perezia macrocephala* (an invalid name). Plants from these populations are readily recognizable because of the smooth, entire leaf and bract margins and the large capitula. Yet, except for the entire leaf margins, these plants are indistinguishable from some Ecuadorian specimens. Thus they appear to be a form of *P. pungens* which has become isolated in the high, moist mountains of southeastern Perú. Moreover, the Cuzco populations are intermediate in morphology between those in northern Perú and those in northern Bolivia, which were described as *P. pungens* var. *cerna* by Rusby in 1896. Rusby's comment, following the description, summarizes well the confusing situation found throughout this species: [this variety] . . . "presents some characters strikingly different from those of the type [of *P. pungens*] but I can not establish specific distinctions." The most conspicuous difference between Rusby's and the typical variety is the presence of nodding heads and deep red-colored bracts in var. *cerna.* Again, both of these characters can be found in specimens from Ecuador. Smooth margined bracts, also present in Rusby's Bolivian plants,

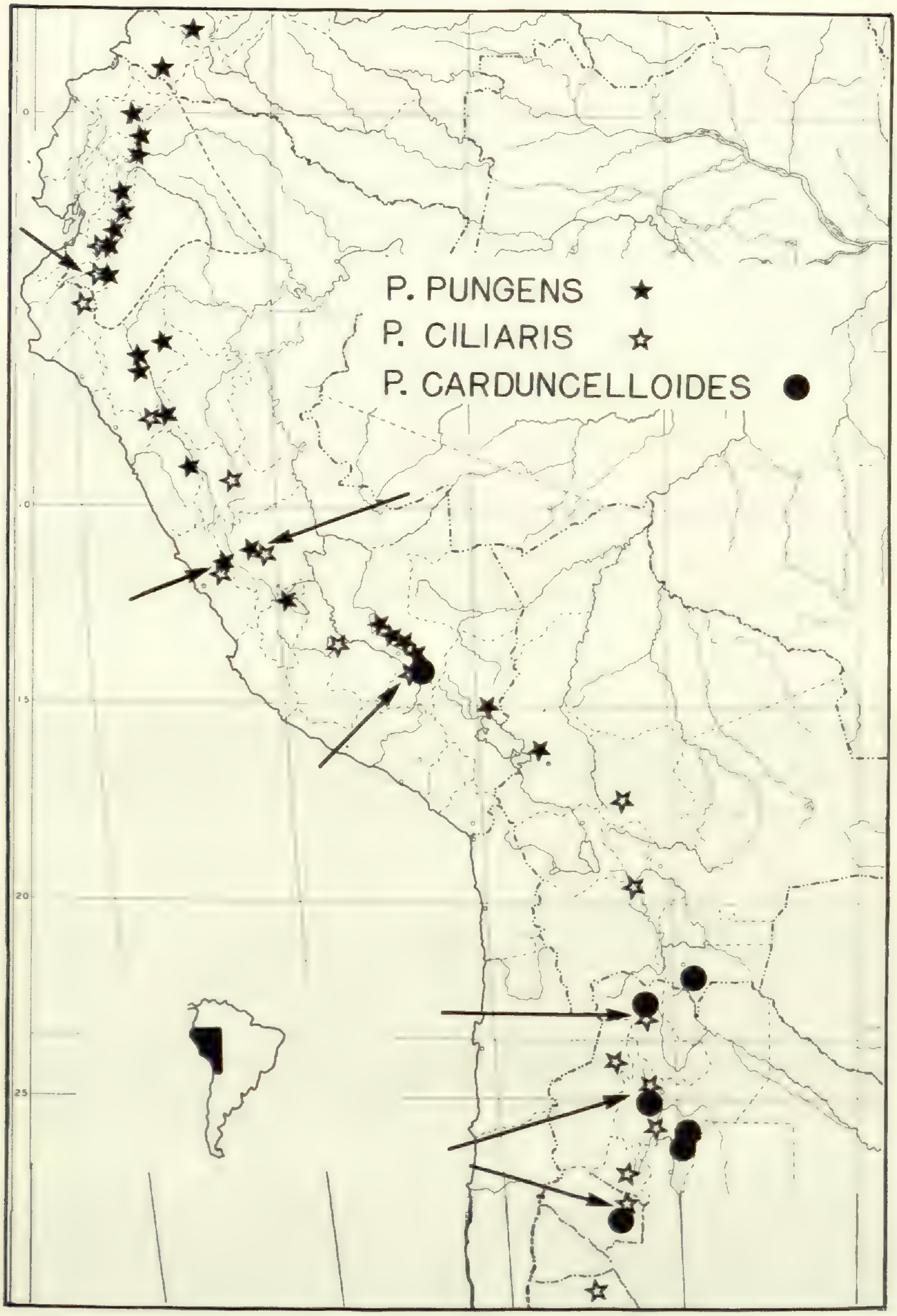


FIG. 21. Distribution of *Perezia pungens, P. ciliaris,* and *P. carduncelloides.* Arrows indicate localities at which intermediate specimens have been collected.

are found in the Cuzco populations discussed above. The type specimens of two other epithets, *P. elongata* O. Kuntze and *P. obtusisquama* Koster are taxonomically the same as Rusby's *P. pungens* var. *cerna* and they have been included under *P. pungens*.

In the Andes, the climate becomes drier south from Ecuador to Perú until, in central Bolivia, the only remaining humid areas are a few east facing slopes. The high puna (except for bogs, which are a specialized microhabitat), which covers most of the central Peruvian peaks and all of the altiplano, is exceedingly dry and covered with short grass. Correspondingly, *Perezia pungens* which seems to inhabit humid slopes, especially those with tall grass, becomes rarer toward the south. Apparently it is replaced by a second, but very similar species, *P. ciliaris*. It appears that in an area of climatic change at the Ecuador-Perú boundary (where the dry upper Marañon creates a sharp dividing line), these two species hybridize. It is possible that *P. pungens* and *P. ciliaris* are merely ecotypes of the same species, and that the intermediate specimens simply reflect a stepped-cline type of variation in an intermediate habitat. Yet, the peculiar distribution of *P. pungens* discussed above and the very distinct habitats preferred by each of the species reinforces the interpretation that they are different taxa. Morphologically, the two are generally separable because *P. ciliaris* has glabrous bracts, achenes, and leaves (or at the most only sparsely pubescent). The edges of the outer bracts are also stiff rather than soft as they are in *P. pungens*, and many specimens have sharp spines along the edges. (Compare PLATE 1–1 with 1–2.)

The following specimens are representative of those found at the Ecuadorian-Peruvian border and which are intermediate in morphology, and, therefore, are presumed to be hybrids between *Perezia pungens* and *P. ciliaris*. ECUADOR. Chimborazo-Cañar: border near El Tambo, 10000–11500 ft, 8–VI–1945, *Camp E–4093* (NY, US). Cañar: neal El Tambo, 9500–10000 ft, 22–IV–1945, *Camp E–2808* (NY). Azuay: Valley of the Ríos Paute and Cuenca, 7200–8000 ft, 13–IV–1945 *Camp E–2572* (NY).

7. PEREZIA CILIARIS D. Don ex Hook. & Arn.

Perezia ciliaris D. Don ex Hooker & Arnott, Comp. Bot. Mag. 1:34. 1835. Lectotype chosen: "CHILE," *Dombey s.n.* (P, G). Hooker & Arnott did not cite a specimen, and obviously took their description from a manuscript of D. Don. They stated that they believed the type to be a Cuming specimen

(not a Dombey). However, I could find no specimen annotated by Gillies, D. Don, or Hooker & Arnott either at Kew or the British Museum. I have, therefore, chosen the Dombey specimen cited by de Candolle as type. It is doubtful if the specimen actually comes from Chile as it is now known.

Clarionea ciliaris (H. & A.) de Candolle, Prodr. 7:61. 1838.

Homoeanthus nivalis Philippi, Anal. Univ. Chile **87**:308. 1894. non *Perezia nivalis* Weddell. Type: BOLIVIA. Oruro: Chayanta between Oruro and Chuquisaca, *without collector* (SGO, Isotype LP).

Perezia foliosa Rusby, Mem. Torrey Club **6**:71. 1896. Type: BOLIVIA. Bolivian Plateau, Turedon, 1891, *Bang 1131* (NY, Isotypes GH, US).

Perezia scapellifolia Koster, Blumea **5**:680. Figure 7 e–i. 1945. Type: BOLIVIA. Cochabamba: high mountain meadow near Compara, 2800 m, IV–1911, *Herzog 1915* (type not seen, Isotype LP).

Perezia scapellifolia Koster var. *parvifolia* Koster, Blumea **5**:680. 1945. Type: BOLIVIA. Cochabamba: Cerro Sipacoya, 3900 m, IV–1911, *Herzog 1915 bis* (type not seen).

Perezia coriacea Tovar, Pub. Mus. Hist. Nat. Lima Bot. **8**:21. Figure 8. 1955. Type: PERU. Huánuco: Mitotambo, above Mito, 3000–3200 m, 24–VI–1953, *Ferreyra 9431* (USM, Isotype GH).

Caulescent, more or less glabrous herbs 10–50 cm tall. Stem leaves scattered up the stem, lanceolate in outline, acute to mucronate, dentate, ciliate, or spiny, clasping. Basal leaves in a loose rosette, petiolate, lanceolate to elliptical, acute, dentate or spiny, or with uneven teeth, 2–5 cm wide, 5–20 cm long. Plants monocephalous or with up to 7 heads per flowering stem. Capitula turbinate, 1.5–3 cm wide, 1–3 cm long, upright. Involucre turbinate, 1–2 cm wide, 1–2 cm long; composed of 3–6 series of bracts. Outer bracts lanceolate, acute, serrate or spiny, or, more rarely, merely stiff with entire margins; 3–4 mm wide, 5–15 mm long, scarious. Inner bracts lanceolate, acute, entire; 1–4 mm wide, 1–2 cm long. Pappus setose, brown, 6–15 mm long. Florets blue. Outer florets 1–3 cm long with ligules 5–15 mm long; from 10–40 florets per capitulum. Immature achenes 1–4 mm long, glabrous or with a few scattered strigose or glandular trichomes. Receptacle glabrous.

Chromosome number: Tucumán, Argentina, $2n=24$.

Distribution: From southern Ecuador south in the high mountains to northern Argentina (Fig. 21). See PLATE 1–2.

Representative specimens: ECUADOR. Cañar: Río Mangan, 20–22 km ENE of Azogues along streams, 3000 m, 5–II–1945, *Fosberg & Prieto 22817* (US). Azuay: valley of Río Paute between Paute and Cuenca, 7200–8000 m, 13–IV–1945, *Camp E–2572* (GH). PERU. Piura: Huancabamba, 8000–9500 ft, 26–IV–1911, *Townsend A215* (F). La Libertad: Llantobamba, 4100 m, 25–II–1950, *Infantes 3676* (LIL); Otuzco, Agallpampa, 3150 m, VI–1950, *Lopez 480* (US). Ancash: Yungay, Llanganuco, 3500–3800 m, *Ferreyra 14357* (GH); entre Casquitambo y Conococha, 3000–3200 m, 24–V–1962, *Ferreyra 14459* (GH). Huánuco: Huánuco, arriba de Mitotambo entre Huánuco y Chavinillo, 3000–3200 m, 24–VI–1953, *Ferreyra 9431* (GH); 15 km east of Huánuco, 1–VI–1922, *Macbride & Featherstone 2116* (GH). Lima: Huarochiri, San Mateo, Río Blanco, above Volcán Mines, 11600 ft, VII, *Saunders 387* (BM). Ayacucho: Huanta & Hacienda Pargora, 4200 m, 2–4–V–1929, *Killip & Smith 23303* (US). Apurimac: Quebrada of Jaccuchic-Chipán, 4200 m, 3–XI–1935, *West 3720* (GH). Cuzco: Chinche, 9 mi from Yanahuanca, 11500 ft, 21–VI–1922, *Macbride & Featherstone 1258* (GH, US). ARGENTINA. Jujuy: Yumbaya, Volcán, 3–II–1929, *Venturi 9173* (US). Salta: Orán, Cerro Queso Asintado, 3100 m, 27–III–1945,

Pierotti 1054 (LIL). Catamarca: Andalgala, 10–II–1947, *Jorgensen 1383* (US); Belén, Las Faldas, Sierra de Belén, 2500 m, III–1938 *Schreiter s.n.* (A, LIL), faldas norte de Portezuelo del Río Blanco de Granadillas, 3100–3300 m, 29–I–1952, *Sleumer & Vervoorst 2588* (US). Tucumán: Sierras Calchaquies, La Puerta, 30–I–1933, *Burkart 5207* (SI), Quebrada de los Alisos, Casa de Piedra, 19–XII–1907, *Castillon 101* (A), El Alazán del Valle, 3200 m, II–1912, *Castillon 2911* (A, LIL), Quebradas del Barón, 3300 m, 7–II–1958, *Fabris 1382* (GH), Cerro Negrito, 3500–3600, 26–II–1949, *Sparre 6139* (LIL), Cerro San José, 3000 m, 11–II–1925, *Venturi 3623* (US), Infiernillo along the road to Amaicha, IV–1965, *Vuilleumier 226* (GH); Chicligasta, Est. Las Pavas, 3200 m, 12–III–1924, *Venturi 3081* (LP, US); Pto. La Cueva, Santa Rosa, 3600 m, III–1924, *Venturi 3201* (GH); Cumbre de Malmala, 3300 m, 3–IV–1904, *Lillo 3429* (A). La Rioja: Sierra Famatina, Laguna Moradita, 13–III–1907, *Kurtz 14601* (CORD), Mina San Juán, 3050–3200 m, 11–II–1906, *Kurtz s.n.* (CORD). Mendoza: Villavicencio, 27–II–1942; *Burkart, Troncoso, Nicora 14416* (SI), Las Heras, 18–I–1943, *Corvas 866* (SI); Cancha de Esquí, 3000 m, 3–II–1950, *Cuezzo & Say 2518* (LIL).

The series of populations included here in *Perezia ciliaris* is very similar morphologically to those of *P. pungens* except that plants of the former tend to be stiffer, less pubescent, and to have more narrow, frequently spiny involucral bracts (PLATE 1–1 and 1–2). The heads of individuals of *P. ciliaris* also tend to be smaller than those of *P. pungens* and, correspondingly, have fewer florets. As mentioned above, an area of hybridization or transition can be seen between these two species in southern Ecuador-northern Perú where the soft, densely pubescent plants of *P. pungens* are replaced by rigid, almost glabrous plants of *P. ciliaris*.

The distribution of *Perezia ciliaris* is in dry areas from southern Ecuador to northern Argentina. However, the range is not continuous but rather composed of small populations isolated in various valleys. The morphological discontinuity frequently seen between individuals from different populations is probably due to limited gene exchange between these disjunct localities. Although described as distinct species in some cases (i.e., *P. foliosa* Rusby, *P. scapellifolia* Koster, *P. coriacea* Tovar), it seems better to consider these populations as allopatric populations or local races of one variable species.

In addition to the apparent hybridization in the north with *Perezia pungens, P. ciliaris* seems to hybridize in Argentina with *P. carduncelloides*. These two species are also very similar morphologically, but they can be distinguished because the latter has large, foliaceous outer bracts which obscure the inner bracts, and yellow or violet florets (compare PLATE 1–2 with 1–3). Plants of

P. carduncelloides appear to grow in more moist habitats than *P. ciliaris.*

Specimens of intermediate morphology between *Perezia ciliaris* and *P. carduncelloides* include: ARGENTINA. Jujuy: Est. Volcán, Abra de Corte, 2500 m, II, *Jorgensen 1383, 1383A* (GH); Loma Negra, 3000 m, 24–III–1934, *Pierano s.n.* (A). Tucumán: Tafí, Macho Rastrojo, 3000 m, 16–II–1920, *Schreiter 1602* (A). Salta: Chicligasta, Est. Las Pavas, 3200 m, 12–III–1924, *Venturi 3081* (LIL). La Rioja: Sierra Famatina, Cuesta de la Tamberia, 7–III–1907, *Kurtz s.n.* (CORD).

8. PEREZIA CARDUNCELLOIDES Griseb.

Perezia carduncelloides Grisebach, Pl. Lorent. 198. 1874. Type: ARGENTINA. Tucumán: Cienega, *Lorentz 320* (photo at GH, Isotype CORD).

Tall, leafy herbs 10–60 cm tall. Stem leaves numerous, scattered up the stem, lanceolate in outline, acute, dentate, clasping and sometimes slightly cordate at the base, light green, surface with few scattered glandular trichomes. Basal leaves usually withered at flowering time; when present, few in number, lanceolate, petioled, dentate, sometimes with a few scattered glandular trichomes; 1–2 cm wide, 5–15 cm long. Plants with 1–7 heads per flowering stem and up to 20 heads per plant. Capitula turbinate, 1.5–4 cm wide, 1.2–3 cm long, upright. Involucre turbinate, 1–2 cm wide, 1–2 cm long; composed of 3–7 rows of bracts. Outer bracts foliaceous, lanceolate, acute or slightly obtuse, dentate, 1–7 mm wide, 6–22 mm long; soft; usually with a few scattered glandular trichomes. Inner bracts lanceolate, acute, entire; 1–3 mm wide, 1–2.5 cm long; stiff, scarious. Pappus setose, brown, 6–15 mm long. Florets yellow or violet. Outer florets 1.3–3 cm long with ligules 5–15 mm long; from 10–40 florets per capitulum. Immature achenes 1–3 mm long; glabrous or with sparse strigose hairs. Mature achenes to 3 mm. Receptacles glabrous or with tufts of white trichomes.

Chromosome number: Jujuy, Argentina, $n=12$. See PLATE 1–3.

Distribution: In southern Bolivia and northeastern Argentina. One specimen of similar morphology has been seen from southern Perú (Fig. 21).

Representative specimens: BOLIVIA. Tarija: Calderillo, 3200 m, 22–III–1904, *Fiebrig 3157* (GH, NY, P, US). ARGENTINA. Jujuy: Tumbaya, Volcán, subida al Cerro Abra Morada, 2600–3200 m, 5–III–1965, *Cabrera & Solbrig 16969* (GH, LP). Tucumán: La Quénoa, 2600 m, III, *Rodriguez 421* (A); Cumbre de Anfama a la Ciénega, 2700 m, 23–III–1922, *Schreiter 3205* (F). Salta: Candelaría, Sierra de la Candelaría, 2500 m, 18–V–1925, *Venturi 3757* (GH, SI, US). Catamarca: Yulayaco, 3500 m, II–1916, *Jorgensen 1380* (GH).

In southern Bolivia and northern Argentina the ecological counterpart of *Perezia pungens* is *P. carduncelloides.* Although specimens are rare, label data indicate that the species frequents moist, grassy slopes as does *P. pungens* in Ecuador and Perú. As is the case also with *P. pungens* and *P. ciliaris, P. carduncelloides* has a range composed of a series of disjunct populations isolated by areas of inhospitable terrain. In areas of southern Bolivia and

northern Argentina where the dry valley bottom habitats meet the upper, wetter grass-covered slopes, *P. carduncelloides* appears to hybridize occasionally with *P. ciliaris*. All of the three species of this complex, *P. pungens*, *P. ciliaris*, and *P. carduncelloides* are similar morphologically and form one of the most confusing taxonomic situations of the South American *Pereziae*. In some ways, it might be better to consider them semispecies as defined by Mayr (1963, p. 671) but only further field studies or experimental work can show whether it would be more meaningful biologically to consider them subspecies rather than distinct species. Morphologically, *P. carduncelloides* differs consistently from the other two taxa in having a paniculate, flat-topped arrangement of heads with usually yellow or violet (rather than blue) florets. The most characteristic feature of *P. carduncelloides* is, however, the presence of very large foliaceous bracts that resemble the uppermost stem leaves. Both related taxa have lanceolate outer bracts definitely smaller than the inner bracts (compare PLATES 1–1 to 1–3).

9. PEREZIA SUBLYRATA Domke

Perezia sublyrata Domke, Notizbl. Bot. Gart. Berlin 13:248. 1936. Type: PERU. Puno: Santa Rosa, 14500 ft, IV–V, *Stafford 345* (K, Isotype BM).

Perezia sublyrata Domke var. *glabrescens* Tovar, Pub. Mus. Hist. Nat. Lima Bot. 8:11, 1955. Type: PERU. Cuzco: Paucartambo, near Quencomayo below Colquipata, 3200–3300 m, 1–V–1925, *Pennell 13789* (GH, Isotypes F, NY).

Decumbent rosette herbs 6-30 cm tall with a rhizomatous root system. Stem terete in cross section, slightly striated and sometimes reddish in color; sometimes with scattered glandular trichomes, especially under the capitulum. Stem leaves 2–9 scattered up the stem, slightly spathulate in outline, acute, slightly spiny along the border, clasping, variable in size, surface usually with multicellular glandular trichomes. Basal leaves few, lyrate in outline, rounded at the apex, dentate with large blunt segments, shortly petioled; width 7–26 mm, length 5.5–21 cm, surface with some glandular trichomes. Flowering stems monocephalous, decumbent or infrequently upright; several flowering stems often present per rosette. Capitula narrowly campanulate, 1–3.5 cm wide, 1.5–2.5 cm long. Involucre elongate, rounded at the base, 1.2–2.5 cm wide, 1.5–2.5 cm long; composed of 4–7 rows of bracts. Outer bracts ovate, acute, entire or slightly dentate at the base, 2–6 mm wide, 7–13 mm long, broadly scarious along the edges, dark green in the center, glabrous or with a few scattered glandular trichomes, often reddish in color or with reddish streaks. Inner bracts ovate-lanceolate, acute, entire, 2–5 mm wide, 14–20 mm long, glabrous or with a few glandular trichomes at the apex; broadly scarious; dark green in the center or slightly reddish in color. Pappus 6–18 mm long, setose, whitish-yellow in color. Florets blue or white; outer florets 1.6–3 cm long with ligules 5–15 mm long; from 18–30 per capitulum. Immature ovaries 2–3 mm long, very slightly

pubescent, or with a fairly dense coating of double hairs. Mature achenes dark brown with a few scattered double hairs; 3–4 mm long. Receptacle slightly convex with a very few glandular trichomes sometimes scattered on the surface.

Distribution: from mid Perú in the province of La Libertad south to northern Argentina in Jujuy (Fig. 22–3). Altitudinal range 3000–5000 m. Flowering from December to May.

Representative specimens: PERU. La Libertad: Huamachuco, Llantobamba, 4100 m, II, *Infantes 3676* (LIL). Junín: vicinity of La Oroya, 13000–15000 ft, *Kalenborn 115* (GH, US). Huancavelica: Huancavelica, Santa Rosa below Huancavelica, 3600–3650 m, 11–V–1958, *Tovar 2971* (GH); Tayacaja between Mariscal Caceres and Pampas, 3450 m, IV–1953, *Tovar 1289* (GH). Puno: Tacaza, 14500 ft, IV, *Sharpe 33* (K). Lago Titicaca, Capachica Peninsula, Camjata Hacienda, 12600 ft, *Tutin 1080* (BM); Moho, *Weddell 4398* (P); northwest of Azángaro, 3900 m, 1–V–1965, *Vuilleumier 246* (GH); Lampa in *Polylepis* association, 4000 m, 2–IV–1951, 4000 m, 2–IV–1951, *Raute & Hirsch s.n.* (NY). BOLIVIA. La Paz: Cerro Quimsachata, 13 km south of Tiaguanaco, 4100 m, 31–III–1936, *West 6390* (GH); Larecaja, Sorata, 3100–3800 m, V–1858–1860, *Mandon 23* (NY, P); 80 km north of La Paz, Mina La Fabulosa, 3–IV–1950, *Brooke 6299* (F, LP); General Campera, 4000 m, 4–III–1921, *Asplund 4900* (US). Chilcani, 3500 m, 2–V–1858, *Mandon s.n.* (P); Marcarmarcani, *Mandon s.n.* (P). ARGENTINA. Jujuy: Tilcara, subida de la Abra de Remante, 4150 m, 25–II–1953, *Sleumer 4075* (LIL).

From the specimens available for study, the distribution of *Perezia sublyrata* appears to be very discontinuous (Fig. 22–3). More collecting at high elevations in the intervening area will show whether or not the species is actually continuous across southern Perú and Bolivia. It is possible that part of the present disruption of the range is due to farming and sheep ranching on the altiplano. I have seen sheep grazing plants of this species in southern Perú (Azángaro), and the Indians there say that plants grow only in the parts of the hacienda which are inaccessible to animals, or have too little vegetation for grazing.

The species most similar in morphology and most closely related to *Perezia sublyrata* is *P. pungens*. The primary morphological characters which separate the two species are the habit and the involucre. Plants of *P. sublyrata* are usually decumbent while those of *P. pungens* are upright, except in Huancavelica, Perú, where the populations of *P. sublyrata* appear to have numerous upright plants. The capitulum of *P. sublyrata* is also much more elongate than that of *P. pungens* and the bracts of the involucre form a pattern of dark green and white in *P. sublyrata* because of the overlapping of bracts with dark green centers and white scarious margins. Finally, the basal leaves of *P. sublyrata* are

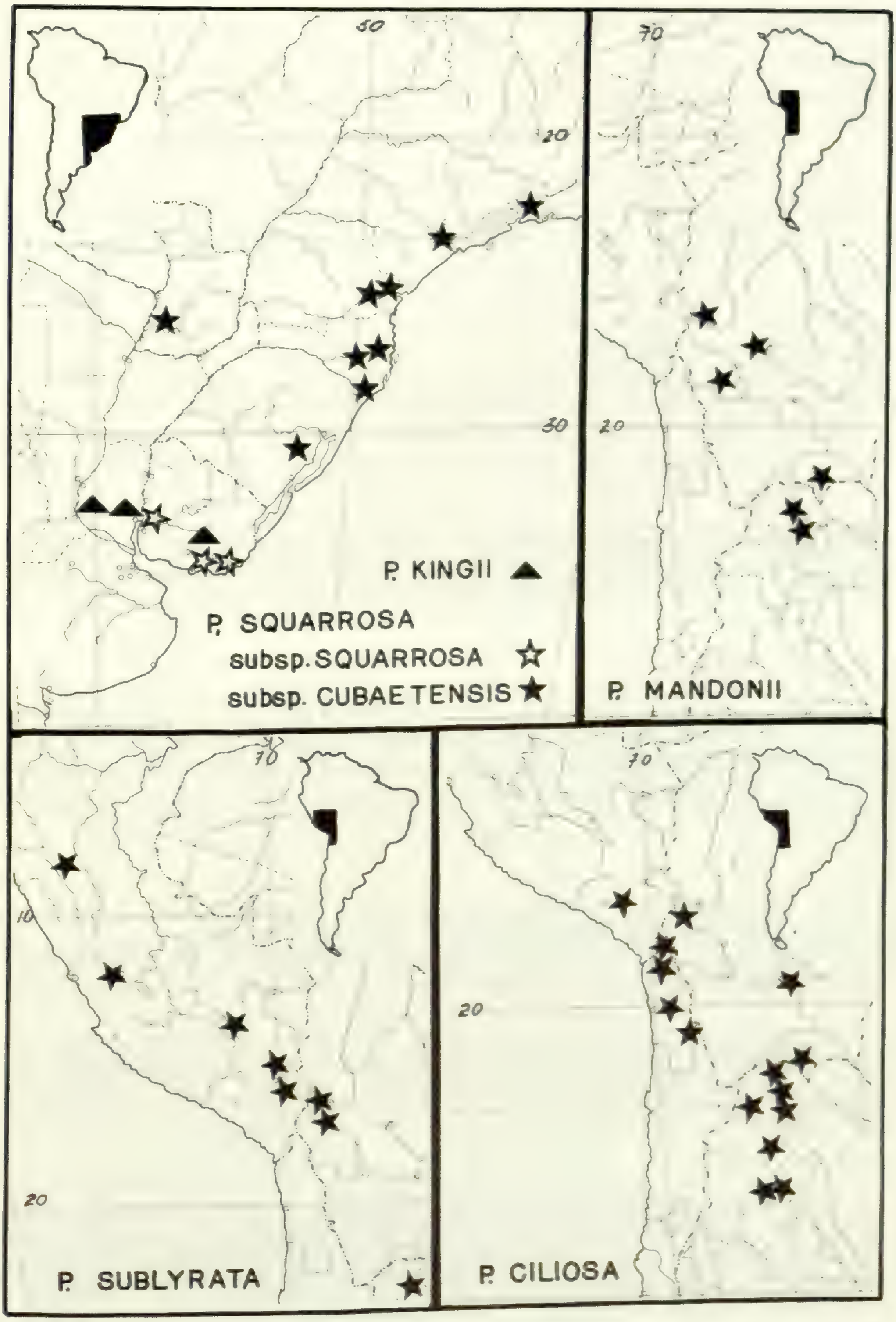


FIG. 22. Distribution of *Perezia kingii* and *P. squarrosa*, both members of the *P. multiflora* species group, and *P. mandonii*, *P. sublyrata*, and *P. ciliosa*, all of the *P. pungens* group.

lyrate with rounded segments and a large terminal segment. The leaves of *P. pungens* are usually lanceolate, although some populations in northern Bolivia have sublyrate leaves.

10. Perezia mandonii Rusby

Perezia mandonii Rusby, Mem. Torrey Club 3(3):66. 1893. Type: BOLIVIA. Oruro: Capí, III–1890, *Bang 777* (NY, Isotypes GH, US).

Perezia laurifolia O. Kuntze, Rev. Gen. 3(2):166. 1898. Type: BOLIVIA. Cochabamba: Pass between Cochabamba and Río Juntas, 4000 m, 13/2–IV–1892, *Kuntze s.n.* (NY).

Small delicate rosette plant 12–38 cm tall with a creeping underground rhizome. Stem glabrous, or, in some populations quite glandularly pubescent at the top under the heads, shiny frequently with red streaks. Stem leaves 5–16 scattered up the stem, usually small and almost scale-like but in some populations becoming long and broad, lanceolate, acute, entire or with small teeth, clasping. Basal leaves linear-elliptical to elliptical, petioled for one-half the length, acute, entire or with a few white small spines along the margin; 0.5–4 cm wide, 7–36 cm long, surface glabrous and shiny, with a few scattered glandular dots, or with a few scattered glandular trichomes. Flowering stems monocephalous. Capitula 1.8–4.0 cm wide, 1.5–3.0 cm long, frequently nodding, campanulate. Involucre turbinate, 1.2–2.5 cm wide, 1.3–2.7 cm long, composed of 4–8 rows of bracts. Outer bracts ovate to lanceolate, acute, entire, 2–5 mm wide, 4–17 mm long, glabrous or with a few glandular hairs, stiff, shiny, broadly scarious along the edges, dark green in the center, frequently with red streaks. Inner bracts lanceolate, acute, entire, 1–4 mm wide, 9–20 mm long, stiff, shiny, dark green in the center, glabrous. Pappus setose, 10–17 cm long, brown-blond or tawny. Florets blue or purple, outer florets longer, 1.7–30 cm long with ligules 6–14 mm, from 16–40 florets per capitula. Immature ovary from 1–3 cm in length, bearing a few scanty strigose hairs, or in some cases some glandular hairs. Receptacle glabrous or in some populations with sparse tufts of white or blond hairs.

Distribution: from northern Bolivia south in the eastern and central Andes to northern Argentina in the province of Jujuy (Fig. 22–2). Altitudinal range from 2500–4500 m. Flowers from January to May.

Representative specimens: BOLIVIA. La Paz: Coroico, vicinity of La Paz, 4500 m, III, *Mandon 24* (NY, P). Cochabamba: Cochabamba, 12000 ft, 27–V–1922, *Cardenas 63 especial* (NY, US); Coloni, 3800 m, IV–1938, *Cardenas 663* (US); road from Cochabamba to Chapare, km 80, IV–1961, *Cardenas 6009* (US); Choro, 17°S by 66°W, 10000 ft, II, *Brooke 6115* (BM, G). Tarija: Calderillo, 3400 m, III, *Fiebrig 2817* (GH, P), 23–III–1924, *Fiebrig 2903* (F, GH). ARGENTINA. Jujuy: entre Santa Ana y Caspala, I–III–1940, *Burkart & Troncoso 11791* (SI); Tumbaya, Volcán, Filo del Vallecito subido al Cerro Horqueta, 3500 m, 5–III–1965, *Cabrera & Solbrig 16966* (GH, LP); Estacion Volcán, Mula Muerta, 3000 m, 15–I–1927, *Castillon 201* (LIL).

In the Andes of Bolivia and northwestern Argentina is a little known species of *Perezia* which was apparently described independently by Rusby in New York and Kuntze in Berlin. Even now collections of *P. mandonii* are scarce, and the exact distribu-

tion and morphological variation of the species are hard to assess.

The specimens from which Kuntze described *Perezia laurifolia* have broader leaves than those from which Rusby described *P. mandonii* a few years earlier. Also, Kuntze's specimens have nodding heads while those of Rusby are upright. However, on all other morphological evidence, the plants of the two collections seem to be conspecific.

I have also tentatively included in this species a series of specimens from northern Argentina (Volcán, Jujuy), although the stem leaves of these specimens are much longer than in any others of *Perezia mandonii* I have seen. At present, the only collections available for comparison are from La Paz (northern Bolivia), Cochabamba (central Bolivia), and southern Bolivia. Future collections from the intervening areas will show whether there are transitions from one series of populations to another, and whether the three groups of populations do, in fact, constitute a single species.

Of the species that grow in the same areas, *Perezia ciliosa* is most similar morphologically to *P. mandonii*. However, the two can usually be distinguished on the basis of the basal leaves. Those of *P. mandonii* have smooth margins with a few short white spines. The basal leaves of *P. ciliosa* are ciliate or dentate. *Perezia pungens* is the only other species of the altiplano region to which *P. mandonii* is similar. However, *P. mandonii* is a shiny, glabrous species whereas plants of *P. pungens* are frequently very pubescent. The outer bracts of *P. mandonii* also make a characteristic pattern of green and white due to the overlapping of bright green bracts sharply edged with white.

A species strikingly reminiscent of *Perezia mandonii*, *P. lactucoides* subsp. *palustris*, is found in southern Chile. There has been little confusion between the two taxa because of the large geographical separation (Fig. 22–2 and 24–1) and their widely divergent habitats. *Perezia lactucoides* grows in marshes and even standing water whereas *P. mandonii* is a high puna grassland species. Morphologically, the achenes of *P. mandonii* are sparsely strigose or have dense glandular trichomes and those of *P. lactucoides* are covered with double hairs. It is impossible to tell whether similarities in morphology between *P. mandonii* and *P. lactucoides* are the result of convergence or whether they reflect some ancestral relationship. At present, it seems that *P.*

mandonii is related to *P. ciliosa* in the *P. pungens* species group and that *P. lactucoides* is better placed in the *P. magellanica* species group.

11. Perezia ciliosa (Phil.) Reiche

Clarionea ciliosa Philippi, Anal. Mus. Nac. Chile 8:35. 1891. Type: CHILE. Tarapacá: Cerro de Copacoya, 3500 m, 18–II–1885, *F. Philippi 2250* (SGO, Isotype LP).

Perezia ciliosa (Phil.) Reiche, Anal. Univ. Chile 116:426. 1905. Fl. Chile 4:444. 1905.

Perezia ciliosa (Phil.) Reiche var. *dentata* Cabrera, Rev. Invest. Agr. Buenos Aires 11:409. 1957. Type: ARGENTINA. Jujuy: Humahuaca, Mina Aguilar, 4650 m, 13–I–1948, *Cabrera 9216* (LP).

Perezia abbiatii Cabrera, Darwiniana 9:52. Fig. 5, A–C. 1949. Type: ARGENTINA. Salta. Poma, Abra del Gallo, 4650 m, 10–II–1946, *Cabrera 9059* (LP).

Small rosette plants with a long thick underground rhizome; plants 3–17 cm tall. Stem terete in cross section, glabrous or with a few glandular trichomes under the capitulum, sometimes slightly striated and reddish in color. Stem leaves 2–11, small and frequently scale-like, lanceolate, acute, ciliate, glabrous. Basal leaves elliptical or lanceolate, acute, densely and evenly ciliate along the margin (dentate in northern Argentina), petioled for almost one-half the length of the leaf; the petiole flared and membranous; leaves 5–20 mm wide, 2–10 cm long, rugose when dry, glabrous. Flowering stems monocephalous, up to 7 flowering stalks per rosette. Individual capitula campanulate, 12–30 mm wide, 10–30 mm long; upright. Involucre turbinate with a rounded base, 9–20 mm wide, 8–21 mm long; composed of 4–6 rows of bracts. Outer bracts ovate, acute, entire or ciliate, 1–3 mm wide, 3–9 mm long, glabrous, up to one-half scarious, frequently reddish along the edges. Inner bracts lanceolate, acute, entire, 1–3 mm wide, 7–20 mm long, glabrous, one-half to almost entirely scarious, often reddish along the margins. Pappus setose, blond-brown, 6–13 mm long. Florets blue or whitish; outer florets 8–25 mm long with ligules 2–7 mm long; from 14–43 per capitulum. Immature achenes 1–4 mm long, covered with long silky double hairs except in some populations where they are only slightly pubescent. Mature achenes 4–5 mm long. Receptacle with tufts of blond hairs around the point of achene attachment.

Chromosome number: Jujuy, Argentina, $2n=24$. (Fig. 5–3.)

Distribution: from southern Perú (Arequipa) south along the Andes at altitudes from 3500 m to snow line, through Bolivia and south into Argentina to latitude 27°S (Fig. 22–4). Flowering from February to April.

Representative specimens: PERU. Arequipa: Volcán El Misti, 15000 ft, III, *Stafford 578* (K). BOLIVIA. La Paz, Vilco, III, *Brooke s.n.* (BM). Potosí: near Potosí, Animas mine west of Chocaya, 4100 m, 21–II–1936, *West 6076* (GH). Tarija: Avilez, Abra Tincuya entre Salitre y Quebrada Honda, 4100 m, 20–II–1953, *Petersen & Hjerling 988* (LIL); Challapata, 4000 m, 1–IV–1921, *Asplund 4899* (US). ARGENTINA. Jujuy: Yavi, Cerro Cajas, 4300 m, 31–I–1953, *Sleumer 3656* (LIL); Mina Aguilar, 4900 m, 22–IV–1965, *Vuilleumier 240, 241, 243* (GH); Tres Cruces, Puente del Diablo, 4000 m, 21–II–1959, *Fabris & Marchionni 1745;* Tilcara, above San Gregorio, 14000 ft, 2–II–1939, *Balls B6005* (F); Humahuaca, Cerro La Soledad, 3500 m,

21–III–1929, *Venturi 8631* (GH, LIL, SI, US); Susques, Cerro Tuzgle, 4800 m, 10–II–1946, *Cabrera 9097* (LP). Salta: Alta Chorrillos, 4560 m, 27–I–1949, *Cabrera & Schwabe 124* (LP). Catamarca: Santa María, Campo Colorado, 4400 m, 3–II–1925, *Venturi 6240* (US). Tucumán: Calchaquies, 15–II–1915, *Castillon s.n.* (LIL), altiplano entre Las Lagunas y Cerro Negrito, 4200 m, 28–I–1952, *Sparre 9368* (LIL). CHILE. Tarapacá: Tarapacá, Cordillera Cerro Columtusca, Apacheta, 4600 m, III, *Werdermann 1109* (F, GH, LIL, LP, NY, SI, US); camino de Putre a Chucuyo, 4100 m, 12–II–1964, *Marticorena, Matthei, Quezada 185* (CONC); camino de Huara a Cancosa, 3850 m, 17–II–1964, *Marticorena, Matthei, Quezada 312* (CONC); camino de Arica al Portezuelo de Chapiquina, 4000 m, 29–III–1961, *Ricardi, Marticorena & Matthei 332* (CONC).

Perezia ciliosa grows at very high elevations, practically at snow line. Individuals are usually hidden under clumps of long, stiff grass such as *Stipa ichu*, or nestled in wet, short grass which makes plants inconspicuous even though they are common.

Despite its wide distribution (Fig. 22–4), *Perezia ciliosa* shows little morphological variation. Within one collection from Tarapacá, Chile *(Werdermann 1109)* there is enough variation to include specimens similar to the type, to plants from La Rioja described as *P. abbiatii* by Cabrera, and to a small form found in northern Argentina and southern Bolivia (recognized as *P. ciliosa* var. *dentata* by Cabrera). The wide spectrum of variation present in this Chilean collection provides evidence that all of the other populations belong in the same species. There is slight clinal morphological variation discernible across the range when each population, as a whole, is compared with neighboring populations. Plants from northern Bolivia and northern Chile have broad leaves with dense, even cilia, and broad, ciliate outer bracts. The La Rioja, Argentina populations are quite similar to those of Chile, but have a larger mean average head size. Presumably, it was this slight shift in size which prompted Cabrera to describe these populations (Abra del Gallo, La Rioja) as a species, *P. abbiatii*. A statistical comparison of the mean head size from populations in La Rioja and Tarapacá showed no significant difference (10 per cent chance that t would exceed the value obtained for head width, and a 70 per cent chance t would exceed the value for head length). This type of comparison should not be interpreted rigidly as a criterion for retaining or submerging taxa, but in this case, all of the other morphological characters of the sets of populations are practically identical.

In Jujuy, northern Argentina, and in adjacent southern Bolivia,

plants of *Perezia ciliosa* are much more delicate in appearance than elsewhere. They have more narrow leaves which are frequently dentate, and almost entire outer bracts. Since the species does not apparently occur in central Bolivia, the northern and southern Bolivian populations represent the extremes in an almost circular type of clinal variation from northern Bolivia west to northern Chile, southeast to La Rioja and northeast to southern Bolivia (Fig. 22–4). A similar kind of variation, although more pronounced, occurs in *P. purpurata*. A reasonable postulate to account for the absence of both these species in southwestern Bolivia is the presence there of wide expanses of salt deserts.

In most cases, *Perezia ciliosa* can be distinguished easily from morphologically similar species, but it has been confused with three other taxa. In Tarapacá, Chile, large plants have been misidentified as *P. purpurata*. The most notable difference between the two species in this area of sympatry is that *P. ciliosa* has entire leaves with dense, even cilia and *P. purpurata* has dentate leaves that are slightly spiny.

In southern Bolivia, some specimens of *Perezia ciliosa* are similar to *P. mandonii* (it is possible that *P. mandonii* may prove to be conspecific with *P. ciliosa* or, at least to be very closely related to it). The most useful morphological character for distinguishing the two species is the leaf margins: those of *P. ciliosa* have cilia whereas those of *P. mandonii* have, at most, a few spines.

The other species to which *Perezia ciliosa* is similar, in general aspect, is *P. coerulescens* because some specimens of the latter have entire leaves with densely ciliated margins. However, the outer bracts of the entired-leaved plants of *P. coerulescens* are quite scarious and ovate in outline. The outer bracts of *P. ciliosa* are non-scarious, green, and very ciliate except in the northern Argentine populations, where the bracts are stiff and lanceolate.

12. Perezia purpurata Wedd.

Perezia purpurata Weddell, Chloris Andina **1**:43. 1855. Type: BOLIVIA. Potosí: au voisinage des lagunes, *d'Orbigny 1420* (P).

Clarionea atacamensis Philippi, Anal. Mus. Nac. Chile **8**:35. 1891. Type: CHILE. Tarapacá: Copacoya, 18–II–1885, *F. Philippi 2250* (LP).

Perezia atacamensis (Phil.) Reiche, Anal. Univ. Chile **116**:425. 1905. Fl. Chile **4**:443. 1905.

Perezia hunzikeri Cabrera, Bol. Soc. Argent. Bot. **3**:161. Fig. 1. 1950.

Type: ARGENTINA. La Rioja: General Sarmiento, El Zanjon, 4000 m, 6–II–1949. *Kraprovickas & Hunziker 5823* (BAB).

Perezia keshua Cabrera, Darwiniana 9:59. Fig. 6. 1949. Type: ARGENTINA. Jujuy: Susques, Quebrada proxima a Susques, 3700 m, 14–II–1945, *Cabrera 8759* (LP).

Rosette plants growing in loose tufts from a thick creeping rhizome with reddish orange roots; plants 6–39 cm tall. Stem terete in cross section, usually densely pubescent with glandular trichomes, sometimes with only a few scattered glandular trichomes. Stem leaves 2–11 scattered up the stem, lanceolate in outline, acute, clasping and slightly saggitate at the base, dentate; usually with glandular trichomes on the surface. Basal leaves few or many forming a dense rosette, but always with petioles which persist after the leaf has decayed causing the rosette to have a thick clump of brown membranous stalks at the base. Leaves lanceolate in outline, acute to mucronate, dentate-spinulose along the margins, narrowing into membranous, broad petioles which are as long as the blade; width 1.5–3.6 cm, length 2.5–24 cm; surface with multicellular glandular trichomes. Flowering stems monocephalous, or in some populations with a panicle of 2–5 heads; several flowering stalks usually present per rosette. Individual capitula campanulate, 2–5 cm wide, 3–3.6 cm long, upright or slightly nodding. Involucres hemispherical to turbinate, 1–4.7 cm wide and 1.5–3.5 cm long; composed of 4–7 rows of bracts. Outer bracts ovate to oblanceolate, mucronate, spiny on the edges, 2–8 mm wide, 7–23 mm long, covered in most populations with a dense covering of long glandular trichomes; scarious along the margins in some populations, frequently reddish in the center. Inner bracts lanceolate, much longer than the outer, acute, entire, 2–7 mm wide, 17–35 mm long, scarious along the margins, sometimes with glandular trichomes at the apex, frequently reddish in the center. Pappus setose, 13–28 mm long, dirty brown in color. Florets white, cream, brown, rose, pink, lilac, blue, or yellow; outer florets 2.3–4.8 cm long with ligules 6–11 mm; ligules frequently with glandular trichomes on the under surface; from 16–76 florets per capitulum. Immature ovaries 1–6 mm long, covered with shiny long double hairs mixed with short glandular trichomes; in some populations the amount of double hairs is reduced or they are completely absent. Mature achenes about 6 mm long, dark red brown, and bearing some long and numerous glandular trichomes. Receptacle with tufts of long shiny trichomes around the points of achene attachment.

Distribution: from central Bolivia southwest into Chile as far as 28° S, and southeastward into Argentina as far south as La Rioja (ca. 30° S) (Fig. 23). Altitudinally from 1500–4800 m. Blooming from January to April.

Representative specimens: BOLIVIA. Potosí: near Potosí, Las Lagunas 4900 m, 3–II–1968, *Vuilleumier 492* (GH). ARGENTINA. Jujuy: Yavi, Cerro Negro, 4000 m, 25–II–1940, *Meyer 22338* (LIL), faldeo de Cerro Poposayo, 4400–4500 m, 1–II–1953, *Sleumer 3680* (LIL); Tres Cruces, Puente del Diablo, 4000 m, 21–II–1959, *Fabris & Marchionni 1736* (LP); Cochirioca, Abra Pampa, 3400 m, 19–II–1929, *Venturi 9375* (GH, LIL, SI, US); Humahuaca, Mina Aguilar, arriba de la mina, 5000 m, 29–III–1952, *Petersen & Pittjerling 153* (LIL); Tilcara, 3000 m, 10–II–1927, *Venturi 6341* (US); Tumbaya, Cerro Moreno, 3500 m, 2–II–1929, *Venturi 9296* (US), 4000 m, 3–II–1929, *Venturi 9455* (US); Laguna Blanca, Portezuelo de Sipán, 3700 m, 20–II–1932, *Kerail s.n.* (LP); Casapalca, cumbres, 3–III–1940, *Burkart & Troncoso s.n.* (SI); Volcán, Abra del Paraguay, 16–I–1920, *Castillon 6881* (LIL). Salta: Caldera, subida al Nevado del Castillo entre Tres Lagunas y las Cuevas, 4200 m, 16–III–1952, *Sleumer & Vervoorst 3008* (US); Sierra

del Cajón, 4800 m, 18–II–1914, *Rodriguez 1376* (SI). Catamarca: Tinogasta, San Francisco, 4200 m, 31–I–1930, *Schreiter 6091* (LIL), Tres Quebradas, 4150 m, 27–III–1951, *Vervoorst 3223* (LIL, P); Belén, Loma Negra, Laguna Blanca, 3300 m, 24–III–1934, *Peirano s.n.* (LIL); Aconquija, 4000 m, 30–I–1933, *Jorgensen 1832* (SI); Valle del Cajón, 4100 m, 22–I–1914, *Rodriguez 1376* (A, LIL); Antofagasta de la Sierra, Incahuasi, 4200 m, 1–IV–1950, *Hueck 510* (LIL). Tucumán: Tafí, Cerro Calchaquíes, 1–I–1915, *Castillon s.n.* (A, LIL), La Puerta, 4000 m, 30–I–1933, *Burkart 5184* (LP, SI); Cerro de la Mina, 3800 m, 14–IV–1924, *Venturi 6331* (US); Río Managua, 2800 m, 28–IV–1926, *Venturi 6906* (US). La Rioja: General Lomadrid, entre Río Las Cuevas y Portillo del Alto, cercanias del Leoncito, 25–I–1949, *Kraprovickas & Hunziker 5593* (LP), cercanias Cerro Bonete, 4500 m, III, *Hunziker & Caso 4164* (CORD, LP), Cordillera el Zanyón, 4000 m, 6–II–1949, *Kraprovickas & Hunziker 5823* (LP). San Juan: Inglesia, Río de las Lagunas entre Puerto del Valenciano y Río de la Sal, 10–II–1950, *Castellanos 15135* (US); eastern part of Cordillera Ortiga, Quebrada Ortiga 3700 m, 14–I–1926, *Johnston 6187* (GH, US); Quebrada del Salto, 16–I–1930, *Perez Moreau 216* (LP). CHILE. Tarapacá: Arica, entre Portezuelo de Chapiquina y Putre, 4000 m, 27–III–1961, *Ricardi, Marticorena & Matthei 220* (CONC). Atacama: Quebrada de Pastos Largos, 4000 m, 26–I–1958, *Behn s.n.* (CONC); Copiapó, Cordillera Río Figuerón, Cerro Paredones, 3500 m, I–1926, *Werdermann 977* (F, GH, HBG, LIL, NY, SI, US); Vallenar, Cordillera Laguna Chica, 4000 m, I–1924, *Werdermann 265* (F, GH, HBG, US), vicinity Lago Valeriano, 4000 m, 8–10–I–1926, *Johnston 6075* (GH, US); Camino al Salar de Maricunga, 4000 m, 31–I–1963, *Ricardi, Marticorena & Matthei 594* (CONC).

The species treated here as *Perezia purpurata* is a confusing one because it is variable morphologically, disjunct geographically (Fig. 23), and there has been misapplication of the names for several isolates. The species essentially consists of four series of populations isolated in different mountain ranges. The first is a series of populations in northern Chile and western Bolivia; the second centers in La Rioja, Argentina; a third, small group is found in the Sierra de Calchaquies (Salta and Tucumán, Argentina); and the fourth is located in Jujuy, northern Argentina.

The confused nomenclature of these various populations should also be discussed briefly. The oldest available name is *Perezia purpurata*, a name given by Weddell to a specimen from Potosí, Bolivia. This name fell into disuse subsequent to its publication—probably because the type specimen was in poor condition and the species was not collected again in Bolivia. Later authors presumably felt that a plant collected once in central Bolivia could not be the same species as the later described *P. atacamensis* Phil., a Chilean taxon known from abundant material.

In February, 1968, I revisted the high puna above Potosí and found plants undoubtedly of the same species as Weddell's from

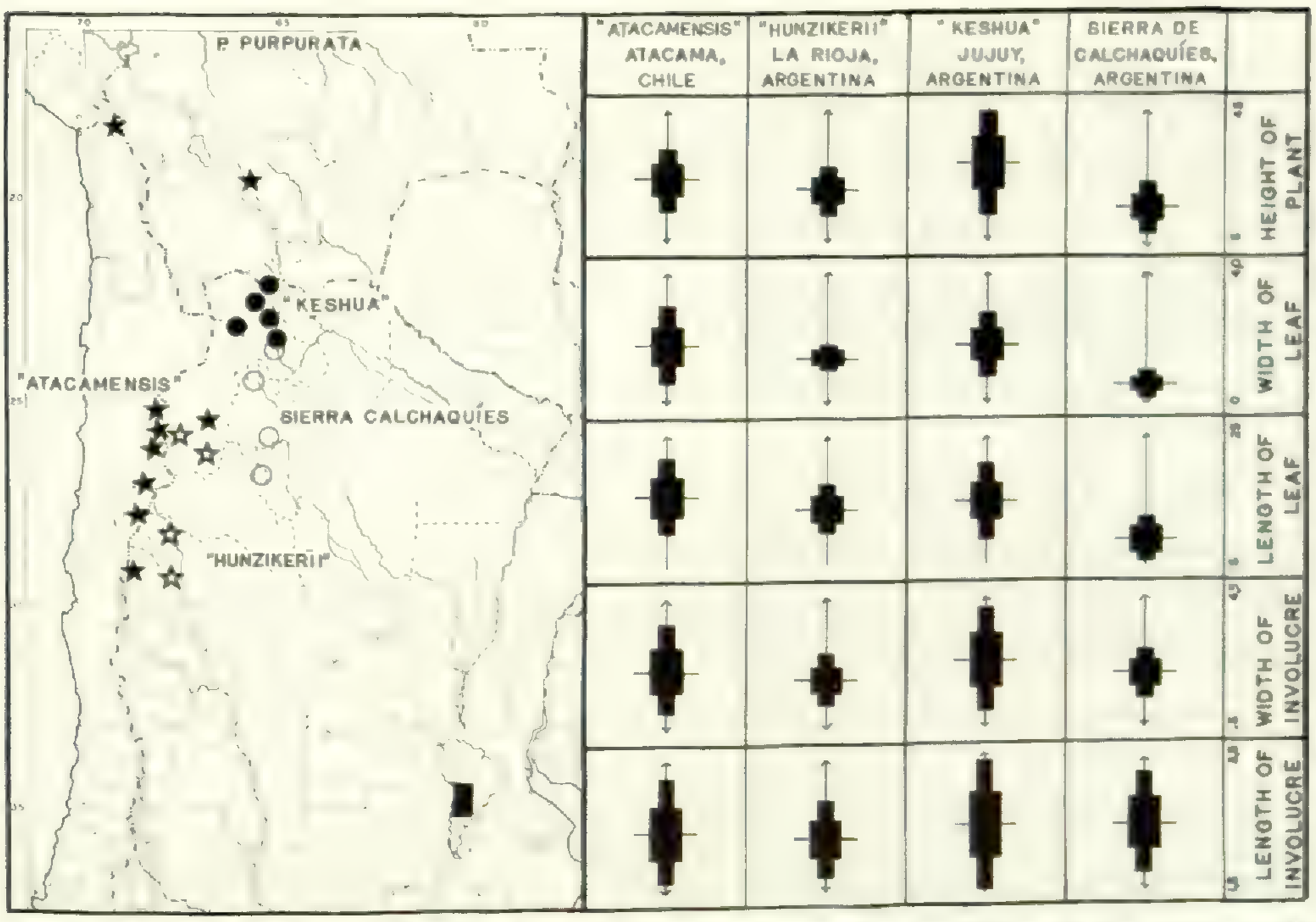


FIG. 23. Distribution of *Perezia purpurata* showing the localities of the four major disjunct groups of populations, and Dice-Leraas diagram of individuals from each of the four areas to show the overlap present in morphological characters (measurements in cm).

this locality. Although plants were very rare (due to sheep grazing), I was able to collect enough material to establish that they were conspecific with plants from Chile. It is still not known whether the apparent disjunction between Tarapacá, Chile and Potosí, Bolivia actually reflects a range disjunction or merely poor collections from the intervening area.

Many years after the description of *Perezia purpurata* (and *P. atacamensis*), Cabrera circumscribed a new species, *P. hunzikeri* from La Rioja, Argentina. Plants from these populations are somewhat smaller than those from Atacama, but the amount of overlap in the dimensions of various parts (organ size is supposed to separate the species) is large (Fig. 23). Since the two sets of populations are practically indistinguishable in all other characters, they are considered here to belong to the same specific taxon.

When he circumscribed *Perezia hunzikeri*, Cabrera described another species, *P. keshua*, from northern Jujuy (Argentina). These plants are distinguishable from those of Chile and La Rioja because they have polycephalous flowering stems and small capitula. It is worthy of note, however, that there is at least one specimen of *P. purpurata* from Atacama, Chile (*Werdermann 265*)

which has a bicephalous flowering stem. The existence of this specimen suggests that the character of polycephalous stems is not sufficient in itself to warrant specific rank. Rather, the populations in northeastern Jujuy seem to be a segment of *P. purpurata* which was isolated in the mountains of this area and has undergone some morphological divergence.

Almost a hundred years after its publication, Cabrera reapplied Weddell's name, *Perezia purpurata,* to a series of populations in the Sierra de Calchaquies (Salta and Tucumán, Argentina). Plants from this area are the most distinctive of any considered here to belong in *P. purpurata* and I consider their inclusion tentative pending further study. A factor which has reinforced the decision to include the Calchaquies populations in this species is the presence of intermediate specimens where plants from this area come into contact with those from northeastern Argentina (the former *P. keshua* populations). Examination of the pollen from intermediates shows that they are male fertile. This zone, without apparent sterility of hybrid plants, indicates that it is an area of secondary contact of imperfectly isolated forms of one biological taxon.

It is suggested here that the present pattern of variation of *Perezia purpurata* is the result of Pleistocene events. A lowering of the snow line during glacial maxima would have allowed the species to occupy, and migrate across, areas now separating the populations. As the ice retreated, populations would have been left stranded on high mountain ranges surrounded by areas of unfavorable habitat. Once isolated, selection by local conditions would have produced some morphological differentiation.

Both morphological and chemical evidence indicate that *Perezia purpurata* is related to *P. pungens* and *P. coerulescens.* Confusing specimens of *P. pungens* can be distinguished from those of *P. purpurata* because the heads of the former are less elongate and its achenes usually have glandular (rather than sericeous) trichomes. Plants of *P. coerulescens* are usually much smaller than those of *P. purpurata* and their basal leaves are less petioled. Moreover, the leaf bases of *P. coerulescens* are not persistent as they are in *P. purpurata.*

13. Perezia pilifera (D. Don) Hook. & Arn.

Clarionia pilifera D. Don, Philos. Mag. 11:388. 1832. Type: ARGENTINA. Mendoza: Andes of Mendoza, El Cerro de la Pulcura, *Gillies s.n.* (K).

Perezia pilifera (D. Don) Hooker & Arnott, Comp. Bot. Mag. 1:34. 1835.
Perezia pilifera (D. Don) Hook. & Arn. var. *nirihuaoensis* Hosseus, Trab. Inst. Bot. Farmacol. 33:101. 1915. Type: ARGENTINA. Río Negro: Cerro Utne, 1800 m, 20–II–1914, *Hosseus 498* (not seen).
Clarionea lechleri Schultz-Bipontinus, Flora 38:122. 1855. Type: CHILE. Magallanes: Sandy Point, *Lechler 1044* (P, Isotypes M, NY).
Homoeanthus humilis Philippi, Anal. Univ. Chile 87:307. 1894. Type: CHILE. Linares: Valle de Bío Bío, Guayeltué, II–1884, *Rahmer s.n.* (SGO).
Perezia linearis Lessing var. *humilis* (Phil.) Reiche, Anal. Univ. Chile 116:428. 1905. Fl. Chile 4:447. 1905.

Tiny rosette plants 2–13 cm tall with a thick woody rootstock. Stem glabrous, sometimes reddish in color, bearing 1–4 scale-like, clasping, acute, glabrous stem leaves. Basal leaves of two types, with only one form on any given plant: either linear, entire, mucronate, and with long, soft white spines along the margins; or, more commonly, with highly dissected leaves, each segment lobed, and each ultimate segment terminated by a long, soft white spine. Leaves from 2–20 mm wide depending on the morph, 1.2–8.5 cm long; both forms glabrous with glandular punctate dots. Flowering stems axillary, one per rosette, monocephalous. Capitula campanulate, narrow at the base, 1–3 cm wide and 1.7–2.8 cm long; upright. Involucres turbinate with a rounded base, 1–2.3 cm wide, 1.2–2 cm long; formed by 3–6 rows of bracts. Outer bracts stiff, lanceolate, mucronate, with long soft white spines at intervals along the edges; 1–5 mm wide, 7–16 mm long; usually glabrous, but rarely with a few scattered glandular trichomes; always with dark red or brownish centers, and scarious along the margins. Inner bracts lanceolate, rigid, acute to mucronate, entire, 1–4 mm wide, 8–18 mm long, glabrous, reddish at the apex, scarious along the margins. Pappus setose, tawny or white, 1–1.6 cm long, abundant. Florets blue, white or pink, sweet smelling; outer florets 1.4–2.4 cm long with ligules 5–10 mm long; about 7–15 per capitulum. Ovaries and achenes covered with very dense, specialized trichomes (Fig. 3–3). Mature achenes 3–4 mm long. Receptacle glabrous or with rings of short trichomes around the ovary bases.

Distribution: an extensive range from San Juán in Argentina to the southern part of Tierra del Fuego (Fig. 26–4). Altitudinal range, 600–4300 m. Flowering from December to March.

Representative specimens: ARGENTINA. San Juán: Dpto. Inglesia, Cordillera de Colanquil, 1887–1888, *Brackenbush s.n.* (CORD). Mendoza: Depto. San Carlos, Laguna Diamante, 3300 m. 4–III–1943, *Covas 1063* (GH), entre el Paso de Portillo y la Laguna del Diamante, Cord. del Portillo de la Llareta, 4300 m, III–1900, *Stegmann 11238* (BAB); alto valle de Camul-có, 14–II–1942, *Burkart, Troncoso & Nicora s.n.* (SI). Neuquén: Parque Nacional Nahuel Huapí, alrededores de refugio Cerro Colorado, 1600 m, 5–II–1951. *Diem 1821* (SI), Cerro Catedral, 1800 m, 7–II–1965, *Vuilleumier 180, 181* (GH). Chubut: north of Lago Futalaufquén, 27–III–949, *Pederson 312* (US). Santa Cruz: Lago Argentino, Río de las Vueltas, arriba de la Est. Pérez, 1200 m, 28–XII–1950, *Sleumer 1372* (US), Est. Fitzroy, arriba de "Chorro," 1200 m, 31–XII–1950, *Sleumer 1417* (US). Tierra del Fuego: Dpto. Ushuaia, Penn. Ushuaia, 11–II–1948, *Vervoorst 202* (LIL). CHILE. Coquimbo: Mailles, 1866, *Bridges 1143* (P); Dpto. Petorca, 5 km south of Junta de Piúquenes, Río Sobrante, 3400 m, 12–II–1939, *Morrison 17293* (F, GH). Santiago: Valle del Río Volcán, 2700 m, III–1933, *Grandjot 1097* (CONC). Colchagua: Cajón del Azufre, II–1831, *Gay 284* (P). Nuble: Termas de Chillán, II–1937, *Jaffuel 3806, 2808* (GH), Pirigallo, 2300 m, 6–II–1936, *Cabrera 3642* (F). Malleco: Lonquimay, Paso Pino Hachado, 31–III–1965, *Vuilleumier 220* (GH). Magallanes: Cerro Guido, Estancia Guido, 750 m,

16–I–1952, *Pfister & Ricardi 463* (CONC, LIL); Ultima Esperanza, Monte Prat, 800 m, I–1950, *Magens 80* (CONC); Las Cumbres Baguales, 500–850 m, 6–II–1962, *Ricardi & Matthei 413* (CONC); Cordillera Señoret, 1000 m, I–1931, *Donat 435* (GH).

This species has the most extensive latitudinal range of any of the Chile-Argentine species of *Perezia,* occurring continuously from about 28°S to 55°S (Fig. 26–4) where numerous plants crowded together form mats in rocky soil above timberline.

The morphological variation of *Perezia pilifera* is checkerboard rather than clinal. Plants from extremely high populations in Mendoza, Argentina are small and have highly dissected basal leaves. In Tierra del Fuego, plants are frequently elongate and their leaves have widely spaced basal segments. However, plants similar to either of these extremes are randomly scattered throughout other parts of the range.

This species exhibits the interesting feature of leaf dimorphism with all of the other characters of the two morphs being identical. The two types of plants are considered polymorphs (in the sense of Mayr, 1963, p. 150–158, 669) because they are "discontinuous phenotypes," i.e., an individual plant has all one type of leaf. No intermediate plants or leaf shapes have been seen and both morphs can grow side by side in the same population. The more common form has highly dissected leaves with fleshy, lanceolate segments each of which ends with a long, soft, white spine. The other morph has linear, needle-like leaves with no, or only a few, scattered white spines. Unfortunately, no experimental work could be done to clarify the genetic system underlying this polymorphism. Populations which contain only one of the two morphs are presumed to have been founded by a propagule(s) genetically capable of giving rise to only one type (founder principle of Mayr, 1963 p. 211).

The entire leaved morph of *P. pilifera,* which Phillippi made a variety of *P. linearis,* superficially resembles species in the *P. recurvata* group. However, the similarity is only in habit and leaf outline. The leaves of *P. pilifera* are thick and fleshy, whereas those of *P. linearis* are soft and flat. The bracts of *P. pilifera* are also quite distinct from those of either *P. linearis* or *P. recurvata* in that they have long, soft, white spines, rather than even cilia or short, rigid spines along the margins. Finally, *P. pilifera* has a unique type of achenial trichome unlike that common to the members of the *P. recurvata* group (Fig. 3–3, Table 3).

It is difficult to determine the relationships of *Perezia pilifera* because it is so distinctive morphologically and its achenial trichome type is unique in the section. On the basis of chemical data, supported by some morphological similarity, it has been placed close to the *P. pungens* and the *P. coerulescens* groups.

14. Perezia carthamoides (D. Don) Hook. & Arn.

Clarionia carthamoides D. Don, Phil. Mag. 11:388. 1832. Type: ARGENTINA. Mendoza: elevated parts of the Andes, Alto de La Laguna, west side of the Cordillera, 1821, *Gillies s.n.* (K).

Perezia carthamoides (D. Don) Hooker & Arnott, Comp. Bot. Mag. 1:34. 1835.

Perezia diversifolia Meyen, Reise um die Erde 1:311. 1834. Type: Destroyed at Berlin. (Photo GH, NY). CHILE. Colchagua: Cordillera de San Fernando, 7–1831, *Meyen s.n.*

Perezia diversifolia Meyen var. *crispa* Meyen, Reise um die Erde 1:347. 1834. Type: CHILE. Colchagua: Cordillera de San Fernando, 7–1834, *Meyen s.n.* (photo GH, NY).

Clarionea carthamoides D. Don var. *crispa* (Meyen) Philippi, Linnaea 33:124. 1864.

Clarionea multicapitata Remy in Gay, Fl. Chile 3:410. 1849. Type: CHILE. Cordilleras, 1839, *Gay* 297 (P, Isotype GH).

Perezia multicapitata (Remy in Gay) Weddell, Chloris Andina 1:44. 1855.

Clarionea spectabilis Philippi, Anal. Univ. Chile 87:303. 1894. Type: CHILE. Coquimbo: Illapel, El Piñon, 1888, *F. Philippi* 2237 (SGO, Isotype LP).

Desert perennial 4–20 cm tall with a long creeping rhizome. Stem terete in cross section, slightly striated, sometimes reddish in color, often with dense glandular trichomes, especially near the capitulum. Stem leaves 1–12 scattered up the stem, lanceolate in outline, acute to mucronate, shallowly dentate with each tooth ending in a sharp white spine; clasping at the base; up to 1.5 cm wide and 3 cm long; sometimes glabrous but more frequently with glandular trichomes. Basal leaves variable in number, lanceolate in outline, mucronate at the tip, margins dentate and spiny; the leaf segments extremely lacerate and tightly curled in some populations. Leaf bases attenuate, slightly flaring, persistent. Width of the leaves 5–38 mm, length 4–21 cm; surface with glandular dots or glandular trichomes. Plants in some populations monocephalous, in others with 2–4 capitula in an upright raceme; up to 17 heads on different flowering stems sometimes present on one plant. Individual capitula campanulate, 1.5–4.5 cm wide, 1.6–3.5 cm long. Involucre hemispherical, 1.5–3.3 cm wide, 1.4–2.7 cm long; composed of 3–7 rows of bracts. Outer bracts oblong to spathulate, mucronate, entire, very scarious along the margins, often reddish in the centers and with glandular trichomes sometimes present at the apex. Pappus setose, 7–22 mm long, tawny, white, or pink in color. Florets blue, white, violet, or coffee-colored; outer florets 6–31 mm long with ligules 5–14 mm long; from 14–35 florets per capitulum. Immature achenes 2–6 mm long, surface with a mixture of double hairs and glandular trichomes. Mature achenes with fewer double hairs and prominent, dark amber glandular trichomes; up to 6 mm long. Receptacle convex with a few scattered trichomes on the surface.

Distribution: in Chile from Coquimbo south in the mountains to Colchagua. In Argentina in the provinces of Mendoza and San Juán (Fig. 27–1). Altitudinal range from 1800–3600 m. Flowering from November to March.

Representative specimens: ARGENTINA. San Juán: Cordillera Real, Paso del Concerro, 16–I–1953, *Castillanos 15137* (US); Portejuelo La Fría, 3600 m, 1–II–1950, *Ruiz 13002* (LIL, LP); Mercedaris, Arroyo Blanco, 1900 m, 29–I–1951, *Semper 13938* (LP). Mendoza: between Puente del Inca and Las Cuevas, 2800 m, 7–I–1956, *Boelcke, Hjerting, Rahn 2180* (LP); camino al Cristo Redentor, 8–II–1921, *Hosseus 2191* (CORD); Tres Esquinas, I–1927, *Carette 410* (SI); Cordillera de Tigre, 2300 m, *King 330* (LP); Los Molles, Vayas altas in arenosis, 13–I–1893, *Kurtz 7557* (NY); Cerro Aconcagua, Valle Horcones, 3000–3500 m, *Leal 155* (LP); Dept. San Carlos, Laguna Diamante, 16 km from Vegas Yauche, 3380 m, 18–I–1963, *Boelcke, Bacigalupo, Correa 10074* (LP); Paso de la Cruz, 2100–3200 m, 15–I–1949, *Leal 11690* (LIL). CHILE. Coquimbo: Dept. Ovalle, Río Gordito, 30–I–1951, *Jiles s.n.* (GH); Dept. Illapel, Cerro La Yerba Loca, two hours by horse east of La Vega Escondida, 22–XII–1938, *Morrison 16948* (GH). Aconcagua: Caracoles, head of the Aconcagua Valley, I–1936, *Jaffuel 3519* (GH). Santiago: Alhué, Monte Cantillana, 2–I–1939, *Barros 2012* (LP, SI); Cajón de Morales, valle de Maipo, 3000 m, 15–III–1921, *Jaffuel 417* (GH); Potero Escondido, 3500 m, II–1947, *Boelcke 2463* (LP); Río Yeso, 17 km de Romeral, 28–XII–1941, *Biese 651* (LIL); hills at Maipo, San Gabriel, 3000 m, I–1939, *Grandjot 3575* (GH); Río Blanco, 3000 m, 17–II–1964, *Boelmer 372* (GH); mountains above Río Colorado, 4500 ft, 15–II–1902, *Hastings 539* (NY); pies de la Sierra Bella, 3600 m, 10–I–1930, *Behn s.n.* (CONC). O'Higgins: Copada, 1750–2000 m, 25–I–1925, *Pennell 12268* (GH, NY); El Teniente near Río Coya, 2700–2900 m, 26–I–1925, *Pennell 12320* (GH); Rancagua, Cordillera de Codegua, 3000 m, 17–I–1945, *Barros 3914* (LP). Colchagua: vegas del Flaco, 1900 m, 18–I–1964, *Marticorena & Matthei 718* (CONC), Cajón de las Damas, XII–1936, *Milner s.n.* (CONC); Cordillera de Tinguiririca, 2100 m, I–1929, *Pirian 61* (GH).

Perezia carthamoides is one of the more showy plants of the dry areas of northern Chile and northwestern Argentina (Fig. 27–1). It is a fairly common species at high elevations in dry or subhumid soil. In the spring it displays large numbers of showy rose, violet, or cream-colored heads, sometimes with several different colors of florets in one population.

Most of the morphological variation within *Perezia carthamoides* is east–west, rather than north–south. Beginning in the Santiago valley area (south to the Baños de Flaco in Colchagua) is a series of populations described as *Clarionea multicapitata* by Remy, which, as the name implies, have an inflorescence of capitula rather than monocephalous flowering stems. Other morphological features associated with these populations include foliage that tends to be lighter green than that of other populations, and glandular dots instead of glandular trichomes on the leaf and bract surfaces.

Despite the fact that plants from this western series of populations are easily recognizable, there is evidence to indicate that they are biologically conspecific with more "typical" *Perezia carthamoides*. All of the "*multicapitata*" populations are found west of the Andes. Going east across the high passes (i.e., between Portillo and Puente del Inca), one finds a gradual morphological transition from the central Chile populations, to those found in Mendoza, Argentina.

At high elevations in Mendoza, at the eastern range extremity, the populations of *Perezia carthamoides* (described as *P. carthamoides* var. *crispa* Meyen) are characteristically compact, and have highly lacerated leaves. These morphological features are probably best explained by the fact that these plants grow at altitudes about 3300 m.

The transition in morphology eastward from central Chile to Argentina indicates that the populations exchange genetic material and should be considered one species. The differentiation which has occurred seems to be the result of isolation of populations to the east and west of the Andes during the Pleistocene, when mountain-top glaciers were low enough to effect such a separation (Brüggen, 1950). Once this barrier was removed, the ranges of the eastern and western populations re-expanded and again came into contact. Although the period of isolation was sufficient to allow some morphological divergence, the populations do not seem to have become reproductively incompatible, and now form intermediates when they come into secondary contact.

Perezia carthamoides shows some morphological resemblances to *P. purpurata* and *P. poeppigii* although it is usually easily distinguishable. It can be distinguished from *P. purpurata* which has softer, pubescent outer bracts, by its stiff, broadly scarious bracts. The heads of *P. purpurata* are also elongate rather than broadly hemispherical as in *P. carthamoides*. *Perezia poeppigii* is easily recognized by its smaller stature, very lanceolate bracts, and turbinate capitula.

Data from chemical analyses suggests that *Perezia carthamoides* is close, at least in phenolic and flavonoid compounds, to *P. poeppigii* and, through it, to the *P. recurvata* species group (Fig. 11 and 12). In morphology also, there is a gradual transition of some characters from *P. carthamoides* to *P. poeppigii* and *P. recurvata*.

Since *P. carthamoides* belongs to the *P. pungens* group, believed to represent a rather ancient assemblage, it could be the modern descendent of the form which gave rise to the *P. recurvata* group.

15. Perezia viscosa Less.

Perezia viscosa Lessing, Synop. Comp. 408. 1832. Type: CHILE. Bío Bío: Meseta de Antuco, XII, *Poeppig 772* (P, Isotypes F, NY).

Homoianthus viscosus (Less.) de Candolle, Prodr. 7:64. 1838.

Clarionia spathulata Lagasca ex D. Don, Trans. Linn. Soc. I. **16**:205. 1830. (non *Perezia spathulata* Philippi) Type: CHILE. *Ruiz & Pavon* (type not seen).

Perezia spathulata (Lag. ex D. Don) Hooker & Arnott, Comp. Bot. Mag. **1**:33, 1835.

Tall, robust plants arising from a basal rosette of few leaves; plants 23–64 cm tall. Stems terete, often striated, covered with long (.5 mm) multicellular glandular trichomes. Stem leaves 2–8 scattered up the stem, lanceolate, acute, minutely dentate, clasping, very variable in size; from 4–5 cm long to almost scale-like; coriaceous with scattered glandular trichomes on the surface. Basal leaves lanceolate to spathulate, acute, subentire, lobate to dentate, attenuate at the base; 1–32 cm wide, 4–28 cm long; frequently glabrous, but sometimes with scattered glandular trichomes. Inflorescence in most cases a loose raceme of 2–4 heads; some plants monocephalous. Capitula campanulate, 2.7–4.3 cm wide, 1.7–2.1 cm long; upright or slightly nodding. Involucre hemispherical to turbinate; composed of 4–6 rows of bracts; 1.2–3 cm wide, 1–2.6 cm long. Outer bracts ovate to lanceolate, acute to obtuse, slightly dentate; 1–4 mm wide, 4–11 mm long; usually non-scarious, but sometimes slightly so along the margins. Inner bracts lanceolate, acute, 1–3 mm wide, 8–14 mm long, scarious along the margins and with glandular trichomes at the apex. Pappus setose, brownish-yellow, 1–1.3 cm long. Florets blue; outer florets 19–25 mm long with ligules 7–14 mm long; corollas with glandular trichomes on the under surface, and in a tuft at the end, of the ligule; about 35–46 florets per capitulum. Immature ovaries covered with dense, silky, white or copper-colored trichomes mixed with glandular trichomes; 2–4 mm long. Mature achenes 4 mm long with a few scattered double hairs and glandular trichomes. Receptacle with short tufts of white trichomes around the point of achene attachment.

Distribution: from Colchagua in Chile south in the *Nothofagus* forest to Osorno. In Argentina in Neuquén, also in the Valdivian forest zone (Fig. 24–2). Altitudinal range from 100–1200 m. Flowering December through March.

Representative specimens: ARGENTINA. Neuquén: Parque Nacional Nahuel Huapi, Cerro Colorado, Portejuelo de los Ardillas, 1200 m, *Diem 27* (LP), Isla Victoria, 12–XII–1944, *Descole 2507* (LIL), shore of Lago Nahuel Huapi, 770 m, 14–I–1934, *Llunger 673* (NY); Mamuil Malal, I–1931, *Joseph 5569* (US). CHILE. Colchagua: Rancagua, *Bertero 702* (GH). Bío Bío: camino de Quilquilco a Laguna Malleco, 950 m, 31–XII–1946, *Pfister s.n.* (CONC, LP). Malleco: Parque Nacional Nahuelbuta, Cordillera, Lago de Cotora, 1200 m, 18–I–1958, *Eyerdam 10358* (NY, US). Cautín: Volcán Llaima, I–1925, *Joseph 3141* (US). Valdivia: Chodhuenco, 8–I–1934, *Montero 1034* (GH); Cordillera de Ranco, XII–1856, *Lechler 233a* (P);

Punahué, 100 m, 15–XII–1938, *Hollenmayer 792* (LP); Hualhuapí, 19–V–1875, *Reed 16* (NY). Osorno: Los Halros, I–1835, *Gay 360* (P).

Like *Perezia pedicularidifolia, P. prenanthoides,* and *P. lactucoides* (subsp. *palustris*), *P. viscosa* is not actually a high Andean species. Its range lies entirely within the *Nothofagus* forest belt below timberline (Fig. 24–2). The distributional boundaries of all of these species are those of the usual Valdivian forest inhabitants.

Morphologically, some plants of *Perezia viscosa* are hardly distinguishable from *P. lactucoides* subsp. *palustris,* and yet other specimens are much more similar to plants of *P. pedicularidifolia.* However, in the Nahuel Huapi (Argentina) area, the three species are sympatric and seem to retain their specific identities. In Chile, the three are more similar morphologically and some hybridization between any two or all three has possibly occurred in the province of Valdivia as Reiche (1905) has previously suggested.

In general, *Perezia viscosa* is very pubescent on the flowering stems and outer bracts whereas *P. lactucoides* subsp. *palustris* has only a few scattered trichomes. The corollas of *P. viscosa* seem always to have some glandular trichomes on the under side of the ligule and in a small tuft at the end of the ligule. These trichomes can best be seen on the top of an unopened floret. I have never observed these hairs on specimens of *P. lactucoides* subsp. *palustris*. The other most conspicuous difference between the two species is the base of the leaf: in *P. viscosa,* it is attenuate and in *P. lactucoides* subsp. *palustris* there is a distinct petiole about one-half the length of the leaf.

The other species to which *Perezia viscosa* is similar is *P. pedicularidifolia* (especially the Valdivian populations). *Perezia pedicularidifolia* is, however, always monochephalous whereas *P. viscosa* frequently has two or more heads per flowering stem. The basal leaves of *P. viscosa* tend to be slightly spathulate as opposed to the lyrate leaves of *P. pedicularidifolia.* The corollas of the florets of *P. pedicularidifolia* are also glabrous rather than glandularly pubescent on the ligule.

16. Perezia lactucoides (Vahl) Less.

Plants extremely variable in size, 8–69 cm tall. Stems arising from a rosette of few leaves, terete, glabrous or with a few scattered trichomes,

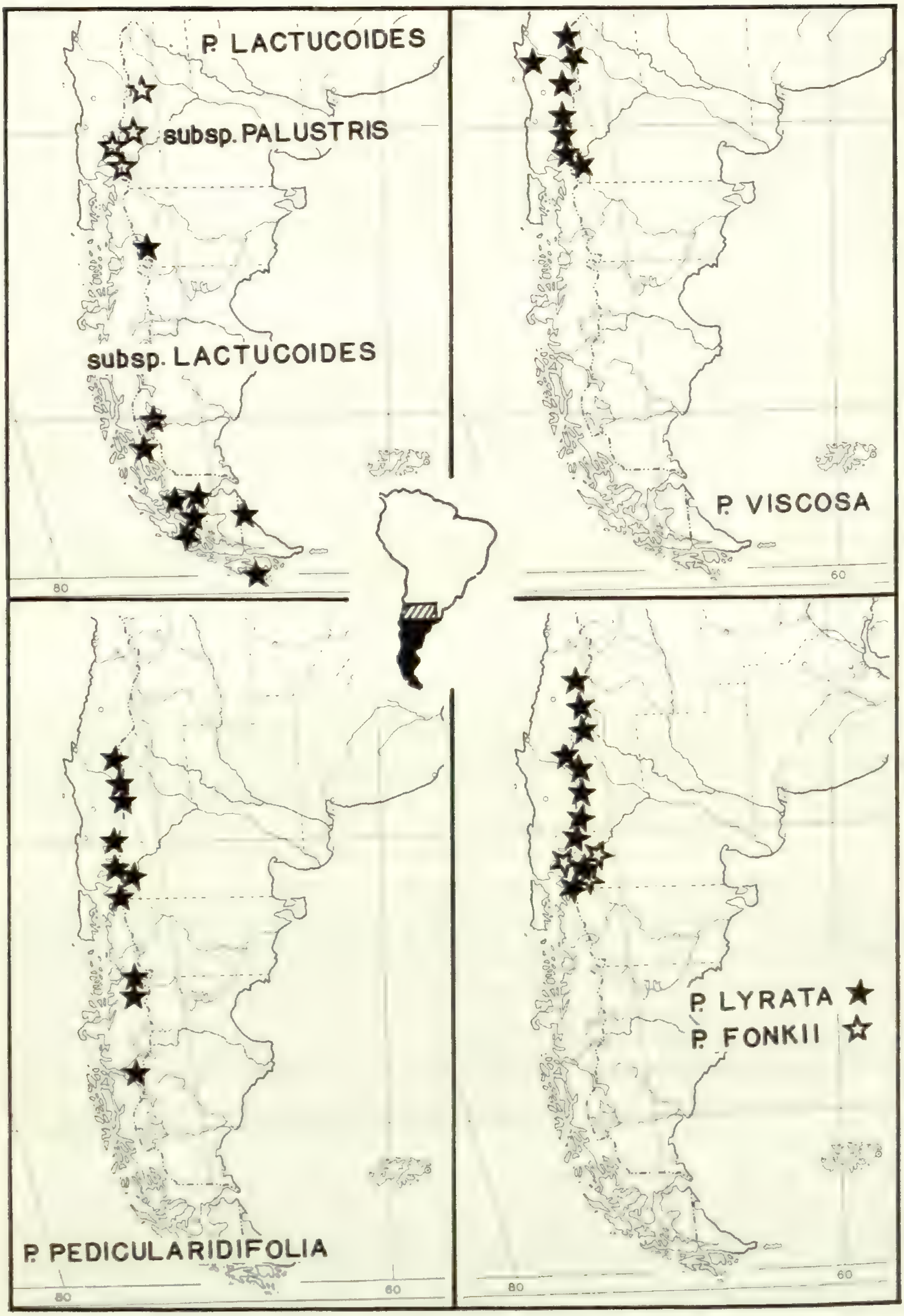


FIG. 24. Distribution of *Perezia lactucoides, P. viscosa, P. pedicularidifolia, P. lyrata* and *P. fonkii,* all members of the *P. magellanica* species group.

bearing numerous (4–15) lanceolate, clasping, acute, entire stem leaves. Stem leaves up to 5 mm wide, to 3 cm long, slightly leathery in texture, glabrous. Basal leaves lanceolate to linear-lanceolate, acute, entire, petiolate for about one-half their length; 2–5 cm wide, 3–28 cm long; usually glabrous but sometimes with a few scattered trichomes. Heads one or two per flowering stem, up to seven per plant. Individual capitula turbinate, 1.5–3.3 cm wide, 1.1–2.3 cm long; upright or nodding. Involucre 1.1–2.5 cm wide, 7–21 mm long, composed of 3–5 rows of bracts. Outer bracts ovate, acute, entire or with tiny serrations; 1–5 mm wide, 4–8 mm long, frequently bicolored with dark centers and lighter, scarious margins; often with a few scattered glandular trichomes. Inner bracts lanceolate to lanceo-linear, acute, entire, 1–4 mm wide, 7–15 mm long, scarious along the margins, glabrous. Pappus setose, tawny, 7–13 mm long. Florets blue, white, or yellow; outer florets 12–23 mm long with ligules 4–12 mm long; 18–35 per head. Ovaries and achenes with a few sparse, long, copper-colored or tawny double hairs, or with dense double hairs. Receptacle with varying amounts of long trichomes.

KEY TO THE SUBSPECIES

A. Florets white or yellow, capitula somewhat nodding, only one capitulum per flowering stem ..... 14a. *P. lactucoides* subsp. *lactucoides*.
A. Florets blue, capitula upright, flowering stems often with two capitula ..... 14b. *P. lactucoides* subsp. *palustris*.

16a. Perezia lactucoides (Vahl) Less. subsp. lactucoides

Aster magellanicus Lamarck, Encyclop. 1:305. 1783. Tableaux. Planche 681 (3). 1797. non *Perezia magellanica* (L.f.) Less. Type: CHILE. Magallanes: Bougainville Bay, X–1767, *Commerson s.n.* (P, Isotypes F, NY). Although this is the oldest name given to this species, the specific epithet is a later homonym for *Perezia magellanica* (L.f.) Less. described in 1781.

Chaetanthera magellanica (Lam.) Sprengel, Sys. Veg. 3:503. 1826.

Homoianthus magellanicus (Lam.) de Candolle, Prodr. 7:65. 1838.

Homoianthus magellanicus (Lam.) DC var. *lactucoides* (Vahl) Hooker, Fl. Antarctica 2:322. 1847.

Perdicium lactucoides Vahl. Skriv. Nat. Selsk. Kiøb. 1:11. Tab. 5. 1790. Type: CHILE. Magallanes: *Commerson s.n.* (C, Isotypes P, F, NY).

Perezia lactucoides (Vahl) Lessing, Linnaea 5:22. 1830.

Clarionia lactucoides (Vahl) D. Don, Trans. Linn. Soc. I. 16:206. 1830.

Clarionea glaberrima Cassini, Opus. Phytol. 2:166. 1826. An illegitimate name because it was superfluous when published. Cassini changed the name of *Perdicium lactucoides* when he transferred the species to *Clarionea*.

Plants very variable in height, some only a few centimeters tall, others up to 50 cm or more. Flowering stems curved, capitula frequently nodding. Outer bracts often reddish or brown in color. Florets white or yellow. Plants frequently becoming black or dark brown upon drying.

Distribution: the southern tip of South America in the provinces of Magallanes in Chile and Santa Cruz and Tierra del Fuego in Argentina (Fig. 24–1). Flowering December to March.

Representative specimens: ARGENTINA. Santa Cruz: Lago Argentino, Reharo, 20–II–1914, *Hicken & Hauman 1123* (SI). Tierra del Fuego: Lago Escondido, 20–I–1960, *Correa & Perez-Moreau 1976* (GH); Ushuaia,

9–I–1960, *Correa & Perez-Moreau 1853* (GH). CHILE. Magallanes: Lago Dickson, 1300 m, II–1931, *Donat 431* (GH, LIL); Isla Hosta, Peninsula Hardy, 2–I–1949, *Vervoorst* 292 (LIL); Punta Brunswick, 500 m, III–1931, *Donat 454* (GH, LIL); Punta Arenas, Seno Otway, 560 m, 1–III–1945, *Biese 1270* (LIL); Cerros Club de Sky, 31–XII–1951, *Pfister s.n.* (CONC).

16b. PEREZIA LACTUCOIDES (Vahl) Less. subsp. PALUSTRIS (Phil.) Vuilleumier comb. nov.

Homoianthus palustris Philippi, Anal. Univ. Chile **27**:316. 1865. Type: CHILE. Valdivia: Cordillera Pelada, I–1865, *Philippi* s.n. (SGO).

Perezia palustris (Phil.) Reiche, Anal. Univ. Chile **116**:424. 1905. Fl. Chile 4:442. 1905.

Tall plants growing in marshy places or standing water. Flowering stems rigid, erect. Outer bracts with dark green centers and white scarious margins. Florets blue or white. Plants remaining green when dry.

Distribution: the lake region of Chile in Valdivia and Osorno and in the provinces of Neuquén, Río Negro, and Chubut in Argentina. Flowering February through March (Fig. 24–1).

Representative specimens: ARGENTINA. Neuquén: 1–VI–1900, *Asp 171* (GH); Lago Lolog, Quelhuenco, II, *Comber 1066* (K); Zapala district, *Epazo 1215* (K). Río Negro: Puerto Blest, 150 m, 15–II–1965, *Vuilleumier 204* (GH); between Puerto Blest and Lago Ortíz Basnaldo, 17–III–1949, *Lourteig 249* (US). Chubut: 19–I–1948, *Kraprovickas 4226* (GH). CHILE. Valdivia: Cerro Mirador, 1250 m, 2–II–1961, *Ricardi & Matthei 5263/66* (CONC). Osorno: summit de la Carpa, 1–II–1958, *Eyerdam 10594* (F, US); Llaima, I–1925, *Joseph 3141* (US).

Hooker noted the extreme variation in plant size present in populations of *Perezia lactucoides* subsp. *lactucoides* as early as 1847, when he observed plants growing in the humid moorlands of Tierra del Fuego and later compared his specimens with those in the Darwinian Herbarium. It appeared to him that there were two distinct groups of plants: one of small individuals, and the other of much taller more robust plants. However, he could find no justification for considering the two forms as separate species. Instead, Hooker (using a typological approach) described the two as varieties of the same species. Today, they are considered to be biological extremes of variation present in one population of one taxon.

Far to the north of Tierra del Fuego is a series of populations which should be considered a subspecies of *Perezia lactucoides*. This group of populations has previously been treated as a separate species by Chilean and Argentine botanists. However, although the northern and the southern groups of populations are widely disjunct, there does not appear to be any valid reason

for retaining them as separate species. The similarity between these populations is between the large plants from Tierra del Fuego and the specimens from the northern Lake Region. Comparison of the small form from Tierra del Fuego with specimens from the northern Lake Region could easily lead to the erroneous conclusion that two taxa were involved.

The only consistent difference between the northern and the southern subspecies is the flower color. *Perezia lactucoides* subsp. *lactucoides* has yellow or white flowers, and *P. lactucoides* subsp. *palustris* has blue or bluish-white flowers. However, several floret colors are frequently found within one species of *Perezia* and it is doubtful if a difference in flower color would be a reliable specific character in this case.

Another species, *Perezia viscosa,* which also inhabits the *Nothofagus* forest region, is very similar to *P. lactucoides* subsp. *palustris.* However, *P. viscosa* has attenuate leaves and densely pubescent foliage and bracts. *P. lactucoides* subsp. *palustris* has petiolate basal leaves and only slightly pubescent foliage. *P. lactucoides* subsp. *palustris* also does not have the glandular trichomes on the ligules as does *P. viscosa.*

17. Perezia pedicularidifolia Less.

Perezia pedicularidifolia Lessing, Synop. Comp. 410. 1832. Type: CHILE. Bío Bío: Andes de Antuco, Pico de Pilque, *Poeppig 824* (P, Isotype NY).

Clarionema humilis Philippi, Linnaea **28**:717. 1858. non *Homoeanthus humilis* Phil. Type: CHILE. Osorno: Volcán de Osorno, II–1852, *Philippi s.n.* (SGO).

Perezia pedicularidifolia Less. var. *humilis* (Phil.) Reiche, Anal. Univ. Chile **116**:434. 1905. Fl. Chile **4**:452. 1905.

Clarionea variabilis Philippi, Linnaea **33**:125. 1864. non *Homoeanthus variabilis* Philippi. Type: CHILE. Valdivia: Cordillera de Ranco, 5000 ft, *Pearce s.n.* (SGO).

Homoeanthus variabilis Philippi, Anal. Univ. Chile **87**:306. 1894. non *Clarionea variabilis* Philippi. Type: CHILE. Valdivia: entre Trancura y Chachim, II–1887, *O. Philippi s.n.* (SGO).

Clarionea parvifolia Philippi, Anal. Univ. Chile **43**:480. 1873. Type: CHILE. Osorno: Cerro Yate, 1871, *Juliet s.n.* (SGO, Isotype LP).

Perezia pedicularidifolia Less. var. *parvifolia* (Phil.) Reiche. Anal. Univ. Chile **116**:434. 1905. Fl. Chile **4**:452. 1905.

Clarionea laciniata Philippi, Anal. Univ. Chile **43**:479. 1873. Type: CHILE. Nuble: Termas de Chillán, 2–II–1862, *Pearce s.n.* (SGO).

Perezia laciniata (Phil.) Reiche, Anal. Univ. Chile **116**:436. 1905. Fl. Chile **4**:454. 1905.

Clarionea Volkmanni Philippi, Anal. Univ. Chile **43**:480. 1873. Type: CHILE. Bío Bío: Trapa-Trapa, *(Volkmann?)* (SGO).

Clarionea comosa Philippi, Anal. Univ. Chile **87**:304. 1894. Type: CHILE. Linares: Termas de Longavi, I–1888, *Schoeneman s.n.* (SGO).

Perezia laciniata (Phil.) Reiche var. *comosa* (Phil.) Reiche, Anal. Univ. Chile **116**:436. 1905. Fl. Chile **4**:454. 1905.

Robust rosette plants about 5–34 cm tall. Stems thick, round in cross section and covered with a dense reddish glandular pubescence. Stem leaves 1–7, lanceolate, clasping, acute, serrate to deeply incised, up to 1 cm wide and 4 cm long; surface covered with glandular trichomes. Basal leaves lanceolate to lyrate, acute, deeply parted to lacerate, 5–18 mm wide and 3.5–10 cm long; leaf surface rugose to glandularly pubescent. Plants invariably monocephalous. Capitula campanulate, 2.5–4.8 cm wide, 1.6–3.1 cm long, upright. Involucre cup-shaped, 1.7–3.4 cm wide, 1.1–1.9 cm long; composed of 3–6 rows of bracts. Outer bracts lanceolate, obovate, or ovate, acute, usually deeply divided into narrow teeth, but sometimes nearly entire with a few serrations; non-scarious and sometimes reddish in color; glabrous or with glandular trichomes. Inner bracts lanceolate, acute, 1–3 mm wide and 8–17 mm long; scarious along the margins. Pappus setose, tawny, 11–17 mm long. Florets blue, violet, or white; outer florets 1.8–3 cm long with ligules 8–18 mm long. Ovaries and mature achenes 2–3 mm long with a mixture of long, tawny double hairs and copper-colored glandular trichomes.

Distribution: from Linares in Chile south to Aysén and east into Argentina in the provinces of Río Negro and Neuquén (Fig. 24–3). Flowering from November to March.

Representative specimens: ARGENTINA. Neuquén: Baños de Copahué, 2000 m, 13–II–1947, *Barba 2103* (LIL); Laguna "Las Monjas," 1550 m, 5–III–1945, *Diem 924* (SI) Río Negro: Parque Nacional Nahuel Huapí, Laguna Frías, Cerro Riggi, 1500 m, 10–II–1940, *Cabrera 6052* (US), Cerro López, I–1960, *Fabris 2170* (LP), Cerro Catedral, 1270 m, 11–II–1965, *Vuilleumier 199* (GH), Cerro Belvedere, 21–III–1934, *Spegazzini 112* (GH). CHILE. Nuble: Termas de Chillán, 1900 m, 5–II–1936, *Cabrera 3609* (F), Valle Hermosa, 2000 m, 1–II–1935, *Pfister s.n.* (CONC). Bío Bío: Trapa-Trapa, *Rahmer s.n.* (SGO). Malleco: Termas de Río Blanco, 1680 m, 3–I–1948, *Behn s.n.* (CONC); Termas de Tolhuaca, 1600–1800 m, 24–II–1925, *Pennell 12763* (F, GH, NY); camino a Paso Pino Hachado, 1300 m, 10–II–1960, *Ricardi & Marticorena 5070/1454* (CONC). Cautín: Volcán Llaima, 1800 m, 31–I–1925, *Joseph 3086* (US), 1300 m, II–1927, *Werdermann 1269* (F, GH, HBG, LP, NY, SI, US). Valdivia: Lago Villarica, I–1931, *Joseph 5813* (US), 1400 m, 5–II–1958, *Hollermayer 786* (LP); Chodhuenco, 1600 m, I–1927, *Werdermann 1384* (F, GH, HBG, LP, LIL, US, NY). Osorno: Volcán Antillanca, 1300 m, 30–I–1961, *Ricardi & Matthei 5221/25* (CONC); Paso Puyehué, 1400 m, 19–III–1954, *Sparre & Constance 10821* (CONC). Llanquihue: Cerro Vicherado, Casa Pangue, 1700 m, 14–I–1953, *Pfister s.n.* (CONC); Volcán Yates, 1400 m, III–1925, *Werdermann 659* (F, GH, HBG). Aysén: east of Puerto Aysén, II–1934, *Pirion 3367* (GH); Portezuelo Los Mallines, entre los valles Simpson y Lbany, 1450 m, 25–I–1939, *Rentzell s.n.* (SI).

Perezia pedicularidifolia is one of the most common species of *Perezia* found throughout southern Chile, where it grows both on exposed slopes and within the *Nothofagus* forest (Fig. 24–3). During the summer, its blue flowers form solid patches on the forest floor of Volcan Llaima.

The large number of epithets given to populations of *Perezia*

pedicularidifolia give some indication as to the variability of the species and the presence of morphologically distinguishable populations throughout the range. As Fig. 20 illustrates, plants of this species tend to be slightly smaller in the northernmost part of its range, then increase in size southward, and, finally, again decrease in size from the north-central part of the range to the southern extreme. The northern populations are probably smaller because of the increased dryness of the habitat as one goes north. The plants from these northern populations (described as *C. laci-nata* Phil.) also tend to have deeply toothed outer bracts and finely dissected basal leaves, characteristics frequently associated with dry conditions.

The plants from Bío Bío south through Valdivia (former *C. volkmanni* Phil.) are, for the most part, tall and robust with large, showy heads. From Valdivia (40°30′S) toward the southernmost part of the range, the average size of plants in the populations again decreases (Fig. 20). In this case, the lower mean annual temperature correlated with higher latitudes probably accounts for the overall smaller plant size. Interestingly, the bracts of the most southern populations (=*C. humilis* Phil.) are almost as dissected as those of the northern populations.

Since the majority of the changes in morphological characters (e.g., size and amount of dentition of the bracts and leaves, and plant size) form a discernible clinal series correlated with geography, I see no reason to give formal recognition to any of the various populations.

There is a possibility that the isolated populations in the Cordillera de Ranco and Lago Villarica of Valdivia are distinct enough to be considered a subspecies of *Perezia pedicularidifolia*. However, I have seen only two collections from this area and there is considerable difference between them.

Difficulty is frequently encountered in separating *Perezia pedicularidifolia*, *P. lyrata*, *P. fonkii*, and *P. viscosa*. The four species are quite similar morphologically and are obviously closely related. Reiche (1905, p. 420) suggested that intermediates were formed between *P. pedicularidifolia*, *P. lyrata*, and *P. fonkii*, but I have seen no specimens that were undisputed hybrids. Yet, populations in the areas where the three species are sympatric tend to be the most confusing, lending some evidence to Reiche's suggestion.

Usually *Perezia pedicularidifolia* differs consistently from *P.*

fonkii in having robust flowering stems, more numerous stem leaves, and lanceolate, rather than spathulate (as in *P. fonkii*), stem leaves. The outer bracts of *P. pedicularidifolia* often tend to be red-purple in color while those of *P. fonkii* are green or dull brown. Both *P. fonkii* and *P. lyrata* often have more than one flowering stem per rosette, whereas *P. pedicularidifolia* invariably has only one. The bracts of these species are not as deeply lacerated as they usually are in *P. pedicularidifolia*.

18. Perezia lyrata (Remy in Gay) Wedd.

Homoianthus lyratus Remy in Gay, Fl. Chile 3:418. 1849. Type: CHILE. Colchagua: Talcaregue, II–1831, *Gay* 283 (P, Isotypes F, G).

Perezia lyrata (Remy in Gay) Weddell, Chloris Andina 1:42. 1855.

Homoianthus gayanus Remy in Gay, Fl. Chile 3:419. 1849. Type: CHILE. Colchagua: Talcaregue, II–1831, *Gay* 282 (P).

Clarionea pinnata Philippi, Linnaea 28:718. 1858. Type: CHILE. Linares: Cordillera de linares. I–1856, *Germain s.n.* (SGO).

Perezia pinnata (Phil.) Reiche, Anal. Univ. Chile 116:435. 1905. Fl. Chile 4:453. 1905.

Homoeanthus capito Philippi, Anal. Univ. Chile 87:309. 1894. Type: CHILE. Bío Bío: Cordillera de Antuco, Trapa-Trapa, II–1881, *Sage* 2256 (SGO, Isotype LP).

Perezia capito (Phil.) Reiche, Anal. Univ. Chile 116:432. 1905. Fl. Chile 4:450. 1905.

Robust herbs 8–28 cm tall. Stem terete, often reddish in color and with glandular trichomes especially under the capitulum. Stem leaves 1 or 2, alternate, spathulate to somewhat lanceolate, acute to obtuse, entire to dentate, clasping, up to 1 cm wide and 3.3 cm long; sometimes covered with glandular trichomes. Basal leaves few in number, acute, lyrate, lobate or parted, if parted the segments slightly dentate; 2–26 mm wide, 5–13 cm long; some with only a few glandular trichomes, others with very dense trichomes. Flowering stems monocephalous, but frequently with more than one stem per plant. Capitula campanulate, 2.4–5 cm wide, 1.6–5 cm long; upright. Involucre hemispherical or slightly turbinate, 1.7–3.5 cm wide, 1.2–3.3 cm long; composed of 4–5 rows of bracts. Outer bracts variable in size and shape, almost orbicular or spathulate to oblong or lanceolate, acute or obtuse, entire to slightly dentate, 1–10 mm wide, 5–22 mm long; covered with glandular trichomes sometimes slightly reddish in color. Inner bracts ovate or linear-lanceolate, acute, 2–6 mm wide, 9–20 mm long, sometimes with a few scattered glandular trichomes at the apex; slightly scarious along the margins. Pappus setose, dull brown, 1.1–1.7 cm long. Florets blue, violet, white or lilac, the outer florets 2.2–3.1 cm long with ligules 9–15 mm long; about 34–54 per capitulum. Immature ovaries 2–3 mm long, bearing a fairly dense covering of copper-colored double hairs, in some populations with glandular trichomes and no double hairs. Mature achenes up to 4 mm long, with fewer of the same type of trichomes. Receptacle convex, tufted with short golden trichomes around the points of achene attachment.

Distribution: Chile from Colchagua south in the Andes to Malleco. In

Argentina in Neuquén. (Fig. 24–4). Flowering January to March. See PLATE 1–5.

Representative specimens: ARGENTINA. Neuquén: Dpto. of Minas, valle superior del Arroyo Atreuco, 2010–2050 m, II–1964, *Boelcke, Correa & Bacigalupo 1150* (LP); Termas de Copahué, 2200 m, 18–II–1940, *Cabrera 6216* (F, LP); Zapala district, *Comber 1234* (K); Cerro Chapelco, 1700 m, 8–II–1955, *Jouskoj 40* (LP); Lago Villarino, 1896, *Roth s.n.* (LP); Lago Lacar, 1896, *Roth s.n.* (LP); Parque Nacional Nahuel Huapí, Cerro Colorado, 1800 m, 11–II–1965, *Vuilleumier 198* (GH). Río Negro: Norquinco, 6500 ft, II, *Comber 527* (K). CHILE. Talca: Paso Pehuenches, 2500 m, 13–II–1963, *Ricardi, Marticorena & Matthei 943* (CONC); Laguna de Maule, 2200 m, I–1943, *Behn s.n.* (CONC). Nuble: Termas de Chillán, 28–II–1947, *Pfister s.n.* (CONC), Prigallo, 2400 m, 6–II–1936, *Cabrera 3656* (F, LP). Malleco: 200 m del limite, 1840 m, 10–II–1960, *Ricardi, Marticorena 5093/1477* (CONC).

As shown in Fig. 24–4, *Perezia lyrata* occurs along the Chilean Andes from Colchagua to Malleco and then appears in Argentina. The species apparently does not grow in Valdivia, but, instead, crosses the Andes at the latitude just above Valdivia and ranges into Neuquén, Argentina. Several other species, *P. pedicularidifolia, P. prenanthoides,* and *P. viscosa* cross the Andes at the same point. The reasons for this distribution are, first, the valleys in the Andean system begin to run east-west rather than north-south as they do farther north (Fig. 1); and second, at about this latitude, the boundary between Argentina and Chile curves to the west, so that most of the mountains are located in Argentina. Therefore, it is natural that a species which follows the Andean chain crosses into Argentina at this point.

Perezia lyrata is a somewhat confusing species because of its wide range of morphological variability. Remy's description was based on a specimen found in the northernmost part of its range where plants tend to be small and more delicate than those further south. The bracts of these northern populations are only slightly spathulate and are quite small. Toward the south, or central part of the range (Fig. 20) the bracts become larger and broader until they are practically round in some populations. However, in Laguna de Maule and Termas de Chillán, from which I have seen good series of specimens, it is obvious that within one population the size and shape of the bracts can range from small and oblong to large and orbicular.

Plants of *Perezia lyrata* also vary considerably in height and, populations with the largest bracts are those which have the tallest plants. A tall, robust specimen with large orbicular bracts

looks very different from Remy's type of the species and one was correspondingly described as *P. capito* Phil. Both Philippi and Reiche (who maintained *P. capito* in the Flora de Chile) listed the amount of dentation of the leaves and the amount of pubescence as further characters for distinguishing *P. lyrata* from *P. capito*. The latter was supposed to have more shallowly parted leaves than *P. lyrata*. Yet, Reiche (1905) noted that the leaves of *P. lyrata* were "polymorphic" in a way that made him think of *Capsella* (Cruciferae). In both *P. lyrata* and *Capsella*, this "polymorphism" is only variation in the size and depth of the leaf dentation. Philippi and Reiche further stated that the foliage of *P. lyrata* was glabrous and that of *P. capito*, pubescent. However, I have seen leaves covered with glandular trichomes in many specimens of the more typical *P. lyrata*. Since there is no consistent character for separating two species, all the populations are considered here as one taxon.

Perezia fonkii and especially *P. pedicularidifolia* are the species most similar to *P. lyrata*. *Perezia fonkii* can be distinguished from the other two by its rounded leaf segments, its delicate flowering stems, its small, thin textured outer bracts, and the absence of glandular trichomes on its achenes. The characters separating *P. lyrata* from *P. pedicularidifolia* are: the habit of *P. lyrata* (PLATE 1–5, i.e., more than one flowering stem per rosette); outer bracts which are spathulate to orbicular; and the basal leaves which are longer in relation to the height of the plant than those of *P. pedicularidifolia*. *Perezia pedicularidifolia* is always monocephalous and has lanceolate bracts which are deeply dissected. Confusing plants from the Ranco and Lago Villarica region of Valdivia with small basal leaves (in relation to the plant size) and lanceolate outer bracts fall more naturally into the combination of characters associated with *P. pedicularidifolia* (see above) than with *P. lyrata*, but it is possible that they are actually hybrids between these two species.

19. PEREZIA FONKII (Phil.) Reiche

Clarionea fonki Philippi, Linnaea **28**:718. 1858. Type: CHILE. Cordillera del Doce, 5000 ft, II, *Fonk* 59 (SGO, Isotype LP). Reiche corrected the spelling of the specific epithet (see below) to *P. foncki* when he placed the species in *Perezia*. However, especially in view of the fact that the collector's name on the type specimen is given as Dr. Fonk, the original spelling of Philippi should be retained.

Perezia foncki (Phil.) Reiche, Anal. Univ. Chile **116**:434. 1905. Fl. Chile **4**:452. 1905.

Clarionea affinis Philippi, Anal. Univ. Chile **43**:479. 1873. Type: CHILE. Cordillera del Doce, 5000 ft, II, *Fonck s.n.* (SGO).

A rosette perennial herb 9–19 cm tall with a rhizomatous root system. Stems terete and covered with glandular trichomes. Stem leaves absent or two or three alternately arranged up the stem; if present spathulate in outline, acute, dentate, up to 4 mm wide and 2.5 cm long; surface covered with glandular trichomes. Basal leaves lanceolate in outline, acute to obtuse, deeply lobed with the lobes sometimes overlapping, narrowing at the base; 10–19 mm wide, 6–12 cm long; surface with glandular trichomes. Heads one per peduncle, but usually 2 or 3 per plant. Capitula slightly campanulate in outline, upright, 2.8–4 cm wide, 1.5–2.6 cm long. Involucre campanulate, 1.4–2.8 cm wide, 1.4–2.5 cm long; composed of 3–4 rows of bracts. Outer bracts lanceolate to ovate, acute or obtuse, slightly serrate or ciliate; non-scarious, 1–5 mm wide and 9–15 mm long; surface with glandular trichomes. Inner bracts lanceolate, acute, entire, scarious along the margins, 1–3 mm wide, 4–14 mm long, glandular trichomes usually present at the apex. Pappus setose, pale brown, 1–1.2 cm long. Florets blue, the outer 1.8–2.3 cm long with ligules 8–12 mm long; about 26 florets per capitulum. Ovaries and mature achenes 2–3 mm long covered with silky dense double hairs. Receptacle slightly convex and covered with tufts of short, gold or copper-colored trichomes.

Distribution: limited to the Andes of Chile and Argentina between the latitudes of 40° and 41°S (Fig. 24–4). Flowering from January to March.

Representative specimens: ARGENTINA. Río Negro: Norquinco, *Comber 536* (K); Parque Nacional Nahuel Huapí, Cerro Colorado, 16–II–1953, *Boelcke & Correa 6977* (LP), 1500–1750 m, 5–II–1951, *Diem 1822* (SI), Rincón Grande, I–1962, *Frey de Jones 75* (LP), Filo Machete, Cerro Rothkugel, 1650 m, 11–II–1945, *Diem 931* (SI), Cerro Catedral, 1800 m, 7–II–1965, *Vuilleumier 182* (GH), Cerro López, 1750 m, 28–I–1946, *Boelcke 1963* (LP).

The range of *Perezia fonkii* is limited to a small area of the lake region of Argentina and Chile (Fig. 24–4), where the species grows in shady rock crevices above timberline.

This species is very similar to *Perezia lyrata* and *P. pedicularidifolia*. As mentioned above, Reiche indicated in his discussion of these three species that he had seen what he considered to be intermediates among them. I also think it is possible that the three hybridize, but they appear distinct enough, even in areas of sympatry, to be considered good species.

The delicate habit and colorless trichomes on the stems and bracts distinguish *Perezia fonkii* from *P. pedicularidifolia*, which is a robust species with dense, red, glandular trichomes on the flowering stems. *P. lyrata* is separable because it has basal leaves and outer bracts which are broader than those of *P. fonkii*. In addition, the lobed segments of the leaves are usually relatively

far apart in *P. lyrata* whereas they frequently overlap in specimens of *P. fonkii.*

20. Perezia delicata Vuilleumier sp. nov.

Planta parva, rosulata, tenella, 10–30 cm alta. Caulis in sectione transversali rotundus, nonnunquam trichomatibus glandulosis sub capitulum. Folia caulina 1–2, lanceolata, acuta, subdentata, amplexicaulia, parva, plerumque glabra. Folia basilia 4–5, lanceolata vel lyrata, non profunde dentata, segmentis interdum dentatis, ad basim attenuata, in textura tenuia, 6–15 mm lata, 2.5–8 cm longa, plerumque glabra, interdum trichomatibus paucis. Capitula in caulem 1, 2.8–4.5 cm lata, 2–3 cm longa, recta. Involucrum hemisphaericum vel subturbinatum, 1–3 cm latum, 1–2 cm longum, phyllariis 3–5–seriatis. Phyllaria externa lanceolata, acuta, integra vel serrulata, 1–8 mm lata, 6–17 mm longa, trichomatibus glandularibus paucis dispersis; venis saepe linea atrofuscata parallela simulantibus. Phyllaria interna lanceolata, acuta, 1–2 mm lata, 1–2 cm longa, trichomatibus glandulosis paucis ad apicem, tenuia, sicut striata per venas. Pappus sparsus, setosus, substramineus, 1–1.4 cm longus. Flores caerulei, 1.8–3.1 cm longi, ligulis, 1.7–2.9 cm longis, glabris, circa 22 in capitulum. Achaenia immatura 1–3 mm longa, pilis duplicatus, longis, sericeis. Receptaculum brevicaespitosum, trichomatibus substramineis.

TYPUS: ARGENTINA. Río Negro: Region del Lago Nahuel Huapí, Paso de las Nubes, 1600 m, 5–II–1940, *Cabrera 5917* (LP, Isotypus US).

Small delicate rosette herb 10–30 cm tall. Stem round in cross section, sometimes with glandular trichomes under the capitulum. Stem leaves 1 or 2, lanceolate, acute, slightly dentate, clasping, small, usually glabrous. Basal leaves 4 or 5, lanceolate or lyrate in outline, acute, shallowly dentate with the segments sometimes dentate, attenuate at the base, thin and delicate in texture; 6–15 mm wide, 2.5–8 cm long; usually glabrous but sometimes with a few scattered trichomes. Heads one per flowering stem, 2.8–4.5 cm wide, 2–3 cm long, upright. Involucre hemispherical or slightly turbinate, 1–3 cm wide, 1–2 cm long; composed of 3–5 rows of bracts. Outer bracts lanceolate, acute, entire or slightly dentate, 1–8 mm wide, 6–17 mm long, with a few scattered glandular trichomes on the surface; veins often appearing as dark parallel stripes. Inner bracts lanceolate, acute, 1–2 mm wide, 1–2 cm long, a few glandular trichomes at the apex, thin in texture and with the dark veins causing them to appear striated. Pappus setose, brownish-yellow, 1–1.4 cm long, scanty. Florets blue, 1.8–3.1 cm long with ligules 1.7–2.9 cm long; glabrous; about 22 per capitulum. Immature achenes 1–3 mm long covered with long silky double hairs. Receptacle with short tufts of tawny trichomes.

Distribution: in the northern Lake Region of Argentina from 900–2200 m elevation (Fig. 25–2). Flowering from January to March.

Representative specimens: ARGENTINA. Neuquén: near Villa la Angostura, 19–II–1952, *Pedersen 1555* (US); Termas de Copahué, 2200 m, 18–II–1940, *Cabrera 6226* (LP); Dpto. Lacar, Cerro Malo, Hua Hum, 19–II–1957, *Hunzicker 6984* (LP); Parque Nacional Nahuel Huapí, Arroyo Minero, 24–II–1953, *Boelcke & Correa 7209* (LP), Laguna las Monjas, en el valle alto del Arroyo Vinagre, 5–III–145, *Diem 917* (SI), valle alto del Arroyo sin nombre 23–II–1941, *Diem 121* (LP), Cerro López, 30–I–1944, *Bernasconi s.n.* (SI), 10–II–1948, *Corte 215* (LP), I–1960, *Fabris 2161* (LP), Laguna

Frías, Cerro Riggi, 1600 m, 10–II–1940, *Cabrera 6058* (LP), Cerro Viola, 1800 m, 24–II–1953, *Diem 2237* (LP), valle alto del Arroyo Goye, 11–II–1914, *Hosseus 165* (LP), Arroyo Constitución, 7–II–1948, *Montiel s.n.* (LP), Cerro El Dormilón, Brazo Rincon, 24–II–1934, *Spegazzini 186* (BAB).

The habitat of *Perezia delicata* appears to be in open areas, perhaps at higher elevations than many of the other species of *Perezia* related to it *(P. pedicularidifolia, P. lyrata,* and *P. magellanica).* Various collectors have noted that their specimens were found in marshy places, possibly accounting for the thin texture of the leaves and bracts common in this species.

Plants placed here in the new species, *Perezia delicata,* have usually been referred by earlier workers to either *P. pedicularidifolia* or *P. lyrata.* However, to me, these plants are very distinct from sympatric representatives of either of these two species. Plants of both *P. pedicularidifolia* and *P. lyrata* are robust and have large, dentate (or undulate) bracts and rather thick textured basal leaves. *P. delicata* has narrow, almost membranous bracts with more or less entire margins. It also has only a few basal leaves and is fragile looking. The heads of *P. delicata* have few florets, but their ligules are long and protrude conspicuously from the involucre. Both *P. pedicularidifolia* and *P. lyrata* have numerous florets per head and much shorter ligules. Finally, both these species tend to have glandular trichomes on the corolla tubes whereas those of *P. delicata* are glabrous.

Perezia fonkii, another similar species, can be distinguished by its lyrate leaves and rounded leaf segments. The basal leaves of *P. delicata* tend to be shallowly lobed and slightly spathulate in outline.

Undoubtedly *Perezia delicata* is closely related to *P. pedicularidifolia, P. fonkii,* and *P. lyrata.* Yet it has a definite geographical distribution, and a consistent set of morphological characters throughout this range. It therefore does not seem to be conspecific with any of these species and should, I feel, be recognized as a distinct taxon.

21. Perezia magellanica (L.f.) Less.

Perdicium magellanicum Linnaeus filius, Supp. Sys. Veg. 376. 1781. Type: Tierra del Fuego, *Forster s.n.* (LINN 1003.5, Isotypes BM, P).

Perezia magellanica (L.f.) Lessing, Linnaea **5**:23. 1830.

Perezia lagascae Cassini, Dict. Sci. Nat. **38**:455. 1825. An illegitimate

name because it was superfluous when published. Cassini explicitly renamed *P. magellanica,* a practice not acceptable under the code.

Clarionea magellanica (L.f.) de Candolle, Prodr. 7:61. 1838.

Clarionea elegans Philippi, Linnaea 28:717. 1858. Type: CHILE. Aysén: Taitao, en los Cerros de Chonos, 500–2000 ft, 3–II–1857, *Fonk 86* (SGO, Isotype LP).

Small delicate plants with a reduced basal rosette, 6–23 cm tall. Stems slender and reddish in color due to a covering of glandular trichomes containing a red pigment. Stem leaves usually absent but in some cases up to 4 in number scattered up the stem; if present, lanceolate to lyrate in outline, acute, deeply serrated, up to 4 mm wide and 1.5 cm long. Basal leaves lyrate, acute, deeply dentate, attenuate at the base, 2–15 mm wide, 8–64 mm long; surface covered with multicellular glandular trichomes. Plants invariably monocephalous with very radiate, usually slightly nodding heads; capitula 2–34 mm wide, 1–3 cm long. Involucre turbinate to slightly hemispherical, 11–22 mm wide, 8–16 mm long; composed of 3–4 rows of bracts. Outer bracts ovate, acute, entire or slightly serrate, 1–3 mm wide, 3–6 mm long, usually with reddish glandular trichomes on the outer surface, slightly scarious along the margins. Inner bracts lanceolate to oblong, acute, entire, 1–3 mm wide, 6–11 mm long, scarious along the margins and slightly reddish in color. Pappus setose, dirty-brown or white, 5–11 mm long. Florets white, the outer much longer than the inner, 1.6–2.3 cm long with ligules 10–18 mm long; about 21 florets per capitulum. Ovaries usually covered with silky white double hairs. Mature achenes to 5 mm long. Receptacle in my specimens covered with short tufts of white or orange trichomes.

Distribution: in extreme southern South America in the provinces of Santa Cruz and Tierra del Fuego in Argentina, and Aysén and Magallanes in Chile (Fig. 25–1). Altitudinal range 250–1400 m. Flowering from October to April.

Representative specimens: ARGENTINA. Santa Cruz: Cerro Fitz Roy, II–1932, *Cabrera B–30* (LP); Viamonte, 27–II–1956, *Goodall 979* (CONC). Tierra del Fuego: I–1769, *Banks & Solander s.n.* (BM, US); Isla de los Estados, *Lillo* (LIL); Puerto San Juán, 31–XII–1933, *Castellanos s.n.* (LP); Mira Monte, II–1954, *Goodall s.n.* (CONC). CHILE. Aysén: Peninsula Taitao, Estero Puelma, 400 m, 26–XII–1945, *Gross 133* (LIL); Region del Lago Buenos Aires, Valle León, 1000 m, 12–II–1939, *Rentzell s.n.* (SI); Puyuhuapí, Cerro Tesoro, 1200 m, 12–II–1940, *Schwabe 75* (CONC). Magallanes: Seno de Agostini, 14–I–1964, *Alvarez 19* (CONC); Seno Otway, Punta Arenas, 1–III–1945, *Biese 1269* (LIL); Isla Diego de Almagro, 11–IV-1945, *Biese 1679* (LIL), 30–III–1945, *Biese 1514* (LIL); Orange Harbor, Smaller Bay, 30–XII–1868, *Cunningham s.n.* (GH); Lago Dickson, 1400 m, II–1937, *Donat 430* (GH, LIL); Glacier del Sapo, 200–300 m, 2–II–1913, *Gasperi s.n.* (CONC); Cook Bay, Seno des Etats, 16–XI–1882, *Hahn s.n.* (P); Otter Bay (Smyth Canal), 23–I–1897, *Jacobsthal s.n.* (HBG); Nicholas Bay, 1841, *Jacquinot s.n.* (P); Monte Prat, 400 m, I–1950, *Magens 70* (CONC); Dpto. Isla Hosta, Peninsula Hardy, Isla Yellow, 2–I–1949, *Vervoorst 290* (LIL).

This tiny, dainty species is found in the Magellanic moorlands of the southern tip of South America and its surrounding islands (Fig. 25–1). Despite the fact that several populations of *Perezia magellanica* are isolated on islands, they show very little morphological variation from one another or from mainland populations.

Two reasons perhaps account for this lack of morphological divergence. First, the Magellanic moorland (a term used by Skottsberg, 1916 and Godley, 1960) is a very uniform habitat. Second, the islands on which the species occurs are near to one another and to the mainland. Very possibly there is some gene exchange between the different insular populations and their continental neighbors.

Perezia magellanica has some peculiar features which readily distinguish it from any of the other species of *Perezia*. The monocephalous stem is covered with a dense coating of long, red-purple, multicellular, glandular trichomes of characteristic structure (Fig. 3–7). The basal leaves of *P. magellanica* are small in relation to the rest of the plant and the heads are fairly large. These two factors give individual plants an almost top-heavy appearance. The outer ligules of this species are much longer than the inner ones and give the heads an extremely radiate aspect. The only species with which it could be confused is *P. delicata*, but the latter does not have the same kind of glandular trichome nor the very radiate capitula of *P. magellanica*.

The corollas of *Perezia magellanica* appear always to be white although they were described as yellow by Vahl (1790) and Lessing (1830).

22. Perezia calophylla (Phil.) Reiche

Homoeanthus calophyllus Philippi, Anal. Univ. Chile **87**:305. 1894. Type: CHILE. Valdivia: Pucaullu, II–1887, *O. Philippi 2254* (SGO, Isotype LP).

Perezia calophylla (Phil.) Reiche, Anal. Univ. Chile **116**:435. 1905. Fl. Chile **4**:453. 1905.

Attractive, large leaved, rosette herbs 8–26 cm tall. Stems usually covered with dense glandular trichomes. Stem leaves numerous, 2–7, alternate; lyrate to broadly ovate in outline, acute, clasping, dentate along the margins; in some specimens up to 1 cm wide and 3 cm long. Basal leaves strongly lyrate in outline, acute, attenuate, parted with the segments composed of dentate lobes; 1.6–2.8 cm wide, 5.8–15 cm long; surface covered with glandular trichomes. Heads 1–6 per stem usually in a cymose inflorescence; individual capitula 2.5–4 cm wide and 1.8–3.2 cm long. Involucres hemispherical to slightly campanulate, 1.5–2.3 cm wide and 1.1–1.7 cm long; composed of 3–5 rows of bracts. Outer bracts lanceolate to ovate, acute to mucronate, dentate, ciliate or entire, 1–3 mm wide, 5–9 mm long; surface with glandular trichomes, sometimes slightly scarious along the margins. Inner bracts linear-lanceolate to lanceolate, acute, entire, 1–2 mm wide, 11–16 mm long, usually scarious along the margins and with a few scattered glandular trichomes. Pappus setose, white or cream in color, 11–13 mm long, scanty. Florets blue, outer florets about 2 cm long with ligules 6–9 mm long; about 20–26 per capitulum. Ovaries and achenes 1–3 mm long, densely covered

with white double hairs. Receptacle flat or slightly convex, covered with short tawny trichomes.

Chromosome number: $2n=24$. Fig. 5–2.

Distribution: in the Andes of Valdivia (Chile) and the mountains of Neuquén and Río Negro (Argentina), see Fig. 25–1. Flowering December through March.

Representative specimens: ARGENTINA. Neuquén; San Martín de los Andes, 2–II–1941,*Bridarolli 2229* (K, LP); Lago Lacar, 1896, *Roth s.n.* (LP); Lago Traful, II–1943, *Soriano 126* (LP). Río Negro: Parque Nacional Nahuel Huapí, Cerro Otto, 8–II–1965, *Vuilleumier 184* (GH), Cerro López, 2080 m, 25–XII–1928, *Cordoni 167* (US), Cerro Leones, 1–I–1934, *Burkart 6227* (LP), Cerro Colorado, 1750 m, 18–I–1951, *Sleumer 1569* (US).

Plants of *Perezia calophylla* grow above timberline near, or in, the crevices of rocks and cliffs in the Lake Region of Argentina and Chile (Fig. 25–1). The species is very localized and appears to be fairly rare in the areas in which it grows. Like several of the species of *Perezia* from the Lake Region, *P. calophylla* was first described from Chile in the Valdivian region, and has not been reported since from that country.

The species to which *Perezia calophylla* are most similar, *P. lyrata, P. fonkii,* and *P. pedicularidifolia,* have been collected sympatric with it in the Parque Nacional Nahuel Huapí (Argentina) and *P. calophylla* can readily be told apart from all these species by its polycephalous flowering stems and numerous broadly ovate stem leaves. The other three species have monocephalous flowering stems and small lanceolate stem leaves. The basal leaves of *P. calophylla* are also characteristic. They are broad, very lyrate in outline, and occasionally, practically diamond-shaped. In some plants, the leaf segments are crowded together and overlapping; in others they are more widely spaced and each is two- or three-lobed with the terminal segment being the largest. This tendency to have lobed leaf segments often gives the leaf the appearance of having a row of mittens along each side of the midrib.

23. PEREZIA BELLIDIFOLIA (Phil.) Reiche

Homoeanthus bellidifolius Philippi, Anal. Univ. Chile 87:306. 1894. Type: CHILE. Valdivia: Cordillera de Valdivia, Huahim, I–1887, *O. Philippi* (SGO).

Perezia bellidifolia (Phil.) Reiche, Anal. Univ. Chile 116:437. 1905. Fl. Chile 4:455. 1905.

Shiny rosette herb 7–24 cm tall. Stems terete with some glandular trichomes below the head; bearing up to 6 alternate, spathulate, acute, entire or undulate, clasping, glabrous leaves. Basal leaves clustered, spathulate, obtuse, undulate to dentate, narrowing at the base, 1.3–2.4 cm wide, 4–9 cm long, glabrous; bright green stem—especially in fresh condition. Campanulate

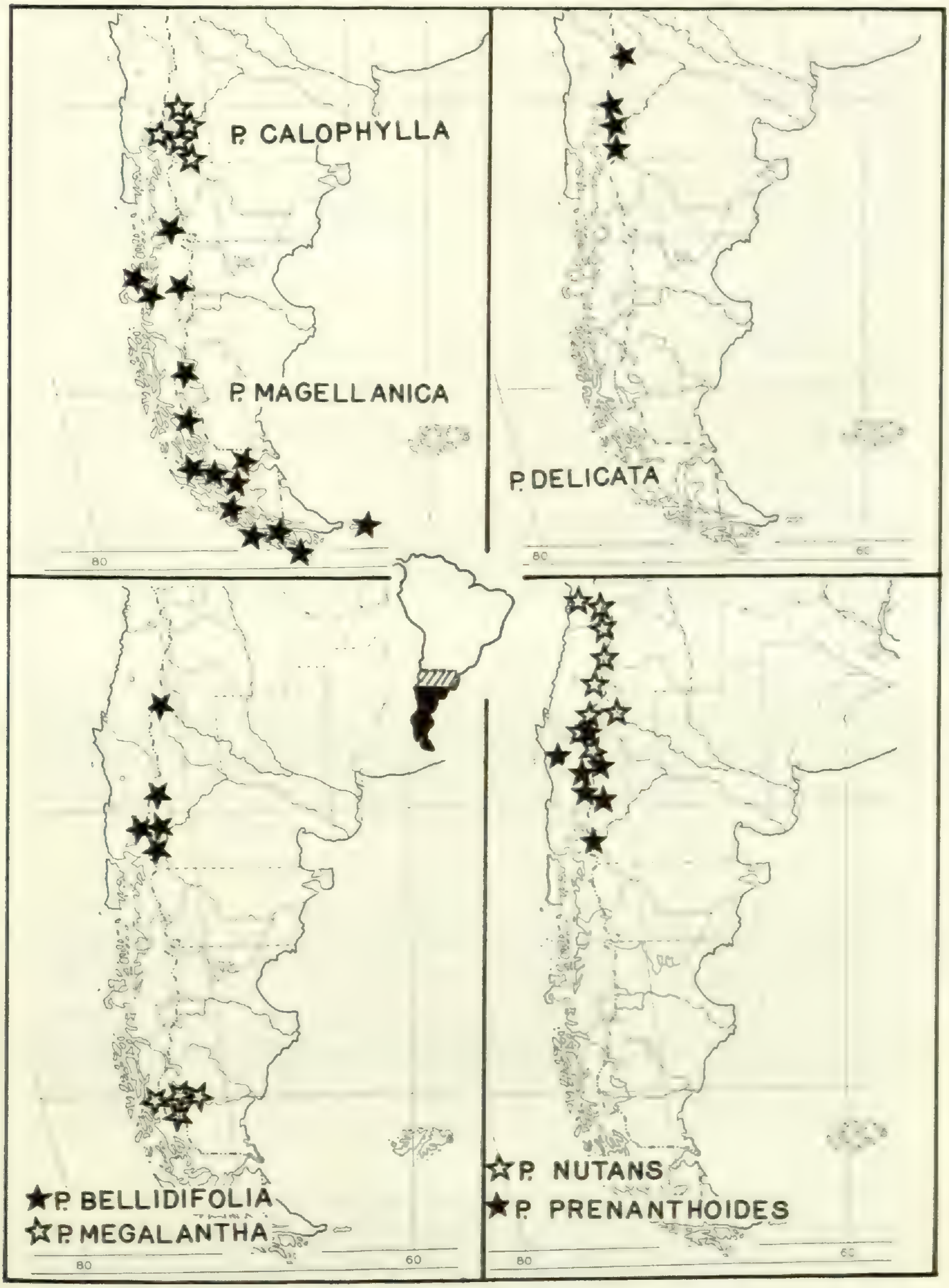


FIG. 25. Distributions of six members of the *Perezia magellanica* species group: *P. calophylla, P. magellanica, P. delicata, P. bellidifolia,* and *P. megalantha.* FIG. 25–4 gives the distribution of *P. nutans* and *P. prenanthoides,* the only two species of the *P. prenanthoides* species group. (See also FIG. 19.)

capitula born singly on each peduncle; up to 6 flowering stems per rosette. Individual capitula 2.5–3.2 cm wide, 1.9–4.5 cm long, upright. Involucre broadly hemispherical, 2.2–2.8 cm wide, 1.5–1.9 cm long; composed of 4–6 rows of bracts. Outer bracts ovate to spathulate, obtuse to acute or even mucronate, undulate or slightly dentate, broadly scarious along the margins, 2–19 mm wide, 11–16 mm long, glabrous or with a few scattered glandular trichomes; green with a few red streaks sometimes present. Inner bracts lanceolate to oblong, acute to mucronate, undulate or slightly dentate at the top, scarious along the edges, 3–5 mm wide, 11–16 mm long, glabrous or with a few scattered glandular trichomes at the apex. Pappus setose, straw-colored, 11–16 mm long. Florets blue, lilac or white, outer florets 1.6–2.3 cm long with ligules 5–11 mm long; about 34–45 per capitulum. Ovaries 2–5 mm long, covered with white double hairs. Mature achenes about 5 mm long, also with white trichomes. Receptacles slightly convex and covered with tufts of white or tawny trichomes.

Distribution: restricted to the central Andes of Chile and Argentina (Fig. 25–3). Flowering December to March.

Representative specimens: ARGENTINA. Neuquén: Colun-Có, 2500 ft, XII, *Comber 872* (K); Sierra Mamuil Malal, *Comber 1098* (K). Río Negro: Parque Nacional Nahuel Huapí, Cerro Catedral, 1800 m, 7–II–1965, *Vuilleumier 183* (GH), Cerro Gutierrez, 1400 m, 25–II–1905, *Buchtein 66* (US); Cerro Meseta cerca del Lago Traful, 1900 m, *Hosseus 1225* (CORD).

One of the prettiest species growing above timberline in the Lake Region of Argentina and Chile is *Perezia bellidifolia*. It usually grows close to snow line in gravel and sand, protected by surrounding rocks (Fig. 25–3) but has been reported once within a forest of *Nothofagus pumilio*. The distributional range of *P. bellidifolia* is very restricted, and only a few collections of the species have been made. Consequently, it shows little geographical variation.

Perezia bellidifolia seems to be related to *P. lyrata* and *P. megalantha*, both of which also have small rosette habits with espinescent leaves and monocephalous flowering stems bearing only one or two leaves, and broad outer bracts. The wide scarious margins of the outer bracts and the shiny glabrous leaves of *P. bellidifolia* easily distinguish it from either of the two related species.

The broadly hemispherical capitula of *Perezia bellidifolia* and its scariously margined bracts are somewhat reminiscent of *P. carthamoides*, a species of northern Chile and northwestern Argentina. The report by Hosseus (1915) of a sepcies in Nahuel Huapí (Río Negro, Argentina) of *Perezia* "aff. *carthamoides*" refers, I believe, to *P. bellidifolia*. Hosseus listed the habitat as dry, rocky soil on the mountain peaks at elevations of 1900–2000 m. The only species at all similar to *P. carthamoides* in such localities is *P. bellidifolia*.

Yet the two are quite distinct morphologically, and probably not related at all. They can be distinguished at a glance because *P. carthamoides* has spiny foliage whereas that of *P. bellidifolia* is entire and smooth.

24. Perezia megalantha Speg.

Perezia megalantha Spegazinni, Rev. Fac. Agron. Vet 3 (30–31):540. 1897. Type: ARGENTINA. Santa Cruz: Lago Argentino, 1884, *Spegazinni 1890* (LP).

Perezia oleracea O. Kuntze, Rev. Gen. Plant. 3(2):167. 1898. Type: ARGENTINA. Patagonia, 1882/4, *F. P. Moreno & Tonini s.n.* (NY).

Small hispid upright herb 7–16 cm tall, arising from a basal rosette of crowded leaves. Roots unknown. Stems terete, covered with glandular trichomes, bearing 0–4 alternately arranged clasping leaves. Stem leaves broadly ovate, acute, dentate, and covered with glandular trichomes. Basal leaves spathulate, obtuse, lobed or dentate, narrowing at the base; 1.1–2.6 cm wide, 3–7 cm long; surface with glandular trichomes. Heads one per flowering stem, up to three per rosette, campanulate in outline, 2–5 cm wide, 2–5 cm long; upright to slightly nodding. Involucres broadly hemspherical, 1.8–3.2 cm wide and 2–3.5 cm long; composed of 4–6 rows of bracts. Outer bracts deltoid, orbicular, or broadly ovate, acute, dentate; 5–18 mm wide, 9–14 mm long; so covered with glandular trichomes that they stick together. Inner bracts spathulate to lanceolate, acute to acuminate, entire, almost entirely scarious; 2–5 mm wide, 13–18 mm long; covered with glandular trichomes and frequently purple tinged. Pappus setose, cream, 9–11 mm long. Florets mauve, lilac, pink or cream; outer florets 2.1–2.7 cm long with ligules 9–14 mm long; about 72–82 per capitulum. Ovaries 3–7 mm long, covered with yellow or copper-colored double hairs. Mature achenes about 7 mm long with more sparse trichomes than the ovaries. Receptacle convex to flat, glabrous and knobby, or covered with short tufts of blond trichomes.

Distribution: restricted to a small area of the Andes near the Chile-Argentina border at the southern parts of Santa Cruz in Argentina, and Magallanes in Chile (Fig. 25–3). Flowering December to February.

Representative specimens: ARGENTINA. Santa Cruz: Lago Argentino, Cordillera Cristales, 2700 ft, 29–XII–1958, *James 3442* (LP); Estancia Stag River, 3500 ft, 26–XII–1957, *Tweedie 213* (K, LP). CHILE. Magallanes: Estancia Guido, 700–900 m, 10–I–1952, *Pfister & Ricardi 12157* (CONC); Dpto. Ultimo Esperanza, Las Cumbres, Baguales, 500–850 m, 6–II–1962, *Ricardi & Matthei 390* (CONC); Cordillera Paine, 1200 m, I–1931, *Donat 402* (GH, LIL, SI).

Perezia megalantha appears to be a very localized species, found growing in rock crevices in a small area of southern Chile and Argentina only (Fig. 25–3). Recently, Thomasson (1959, p. 28) reported the species growing near Bariloche along rapid streams in the Valdivian forest. His report would extend the range of the species northward by almost 800 km. I have seen no specimen from this or any area between the southernmost part of the

continent and Bariloche. Cabrera (1939) did not mention this species in his treatment of the *Compositae* of the Nahuel Huapí National Park. It seems likely to me that a mistake was made in identification and that Thomasson actually collected *P. lyrata* or *P. bellidifolia,* both of which do grow in the national park area.

This species is one of the most unique of *Perezia* in South America, instantly recognized once it has been seen. There is no other species in the genus with such enormous heads, large bracts, and dense covering of very long glandular trichomes. Plants have been described as "sticky" in fresh condition, and in dry specimens it is impossible to separate the bracts without tearing them because they are matted by interlocking trichomes. *Perezia lyrata* also has large heads and bracts which almost equal those of *P. megalantha* in size. Yet the bracts of *P. lyrata* are coriaceous (in the plants from large-headed populations) and are not covered with the same type of trichomes. *Perezia lyrata* may possibly be the modern species most closely related to *P. megalantha.*

25. Perezia coerulescens Wedd.

Perezia coerulescens Weddell, Chloris Andina 1:39. Plate 10 A. 1855. Type: PERU. Cuzco: X–1839–II–1840, *Gay s.n.* (P).

Perezia coerulescens Wedd. var. *amplibracteata* Tovar, Pub. Mus. Hist. Nat. Lima Bot. 8:16. 1955. Type: PERU. Huancavelica: Huancavelica, Huantanayoc-Tansiri, 4400–4500 m, 29–III–1953, *Tovar 1129* (USM).

Perezia nivalis Wedd. Chloris Andina 1:39. 1855. non *Homoianthus nivalis* Philippi. Type: PERU. Carabaya, III–VII–1847, *Weddell 1848* (P).

Perezia integrifolia Wedd. Chloris Andina 1:40. 1855. Type: BOLIVIA. Cochabamba: summit of the Cordillera of Motochata, *d'Orbigny 488* (P).

Perezia cirsiifolia Wedd. Chloris Andina 1:41. 1855. Type: BOLIVIA. Larecaja, Cordillera de Sorata, 5100 m, 1851, *Weddell s.n.* (P).

Perezia violacea Wedd. Chloris Andina 1:42. 1855. Type: BOLIVIA. Potosí: Quebrada de las Lagunas, III, *d'Orbigny 1417* (P).

Perezia nitidifolia Koster, Blumea 5:677. Fig. 5w–z. 1945. Type: BOLIVIA. La Paz: moorland meadows of the plateau of Palca, 3600 m, V–1911, *Herzog 2177* (type presumably destroyed at Berlin, Isotype LP).

Perezia burkartii Cabrera, Darwiniana 9:55. Figs. H–J. 1949. Type: ARGENTINA. Jujuy: high mountains of Santa Ana, 3500 m, 1–III–1940, *Burkart & Troncoso s.n.* (SI).

Small rosette plants appressed to the ground, 1–9 cm tall. Roots long and rhizomatous. Flowering stems monocephalous, usually inconspicuous but occasionally rising above the rosette, bearing 1–6 clasping, lanceolate stem leaves; sometimes reddish in color. Basal leaves several, conferted or in a loose rosette, lyrate to oblanceolate in outline, acute to obtuse, lacerate with spiny segments to undulate; base attenuate, broad, membranous; width 6–26 mm, length 2–11 cm; surface usually glabrous, but occasionally with a few scattered glandular trichomes. Capitula campanulate, 1.2–4 cm wide,

1.2–3.5 cm long, upright. Involucre narrowly hemispherical, 9–30 mm wide, 1.2–2.7 cm long; composed of 4–8 rows of bracts. Outer bracts oblong to ovate, mucronate to acute, dentate and spiny to entire, scarious (often broadly so) along the margins; often reddish in color and with scattered glandular trichomes. Inner bracts lanceolate, acute, 1–5 mm wide, 1–3.4 cm long, scarious, glabrous, pappus brown, 1.1–2.3 cm long. Florets white, yellow, orange, scarlet, maroon, violet or blue; outer florets 1.7–3.3 cm long with ligules 4–12 mm long; from 11–40 florets per capitulum. Achenes usually with some strigose trichomes at the apex and scattered glandular trichomes on the other parts. Receptacle glabrous.

Distribution: mid-northern Perú south through Bolivia into northwestern Argentina at elevations of 3000–5200 m (Fig. 26–1). Flowering occurs from December to July. See PLATE 2–1.

Representative specimens: PERU. Huanuco: 35 mi west of Huallanca, Yanshallas. 16000 ft, 2–X–1922, *Macbride & Featherstone 2481* (F, GH, US). Lima: Valley Rimac, 4900 m, 22–II–1954. *Raube & Hirsch P313* (NY); near Antaicocha, Cerro Colorado east of Canta, 3900–4100 m, 20–VI–1925, *Pennell 14661* (F, GH, NY, US). Junin: near Morococha, 4350–4800 m, 1–V–1942, *Grant 7562* (F), Casapalca, 15500 ft, V, *Macbride & Featherstone 843* (F, GH, US); vicinity of La Oroya, 1918, *Kalenborn & Kalenborn 178* (GH, NY, US). Huancavelica: Huancavelica, Huaytanayoc-Tansiri, puna of Conaica, 4400–4500 m, 29–III–1953, *Tovar 1129* (GH), Tansiri cerca a Manta, 4400–4500 m, 2–IV–1953, *Tovar 1186* (GH); Castrovirreina, Choclococha, 4600–4700 m, 4–V–1958, *Tovar 2888* (GH). Ayacucho: Cangallo, Tojto, 4000 m, *Velarde 5259* (LP). Cuzco: Ollantaytambo, 3000 m, 18–VII–1915, *Cook & Gilbert 1906* (US); Chubamba, 4300 m, 28–III–1962, *Diaz 2025* (LP); Cordillera del Pachatusan, 4400 m, VI–1929, *Herrera 2573* (F); Azuangate, 5700 m, 10–V–1954, *Raube & Hirsch P1136* (NY); Yucay, 4000 m, XII–1937, *Soukup 721* (F); Vilcanota Range, Santa Rosa 14000 ft, II–III, *Stafford 556* (F), La Raya, X, *Stafford 1004* (BM, K); Urcos, 8–12000 ft, V, *Stafford ST23a* (K). Arequipa: Pichu Pichu, 1400 ft, 6–VII–1937, *Stafford 808* (F). Puno: Juro Juro, San Gahan 13000 ft, VI, *Fisher 33* (BM); Santa Lucia, 14500 ft, 11–V–1937, *Stafford 706* (F, K). Crucero Alto, 14700 ft, IV, *Stafford 657* (BM); Azangaro, Salcedo, Mt. Putina, 16–XI–1938, *Vargas 9626* (F, K). BOLIVIA. La Paz: Chacaltaya, 4800 m, II–1908, *Buchtien 1588* (US); highlands at Lake Titicaca, IV–1924, *Buchtien 6803* (NY); vicinity of Sorata near Apacheta de Chacah, 4000 m, IV, *Mandon 18* (F, GH, NY, P, US); top of the pass of the Tipuani-Ancoma-Sorata trail down to Sorata, 16000 ft, 1926, *Tate 822* (NY); Larecaja vicinity of Coroico, Sancha, 3500–4500 m, *Mandon 22* (F, NY, P, US); Songo, XI–1890, *Bang 915* (F, GH, NY, US); mine at the head of the Challana Valley, La Fabulosa, 15000 ft, 26–IV–1950, *Brooke 6317* (BM, F, NY); Paso Tres Cruces road from Cacsata to Quime, 16000 ft, 11–IV–1949, *Brooke 5482* (BM). Oruro: near Araca, tin mine 100 mi from Viloco Oruro via Eucalyptus and Cacsata, 14000 ft, III, *Brooke 5529* (BM). Cochabamba: Chapare, km 75, road between Cochabamba and Tunari, 4000 m, 19–I–1958, *Kraprovickas 8666* (LIL); Grasflur San Benito, 3600 m, 11–VI–1929, *Steinbach 9827* (F, GH, K, NY, US). Potosí: Pacechac, I. *Hill 226* (K). Tarija: Calderillo, 3500 m, 24–III–1904, *Fiebrig 3172* (GH, NY, P, US). Bolivian Plateau, 1891, *Bang 1217* (GH, NY, US). ARGENTINA. Jujuy: Santa Ana, 3500 m, 1–III–1940, *Burkart & Troncoso 11795* (LP, SI); Humahuaca, Tres Cruces, 3400 m, I–1925, *Venturi 10234* (GH). Salta: Orán, Cerro La Escolera, 3800 m, 23–IV–1945, *Pierotti 1348* (LIL); Valle de Cajón, 4100 m, I, *Rodriguez 1373* (A, SI). Tucuman: Sierras Calchaquies, 4000 m, 30–I–

1933, *Burkart 5185* (SI); Tafi, Pabellon, 16–I–1908, *Castillon 97* (F); Cerro Muñoz, Las Animas, 4600 m, 3–I–1916, *Castillon 3304* (LIL); El Alazan, 4100–4200 m, III, *Sparre 8603* (LIL), Quebrada Honda, 3100 m, 24–I–1952, *Sparre 9257* (LIL), Cerro la Mina, Laguna Amarilla, 4000 m, 15–I–IV–1924, *Venturi 6332* (US), Los Chucos, 1–V–1926, *Venturi 6237* (US). Catamarca: Laguna de Tesoro, 4600 m, 3–III–1925, *Venturi 6238* (US); Santa Maria, 4600 m, 1–I–1925, *Venturi 6241* (US).

PROBABLE HYBRIDS BETWEEN PEREZIA COERULESCENS AND P. PINNATIFIDA

PERU. Junin: Mt. La Juntay near Huancayo, 4700 m, 27–IV–1929, *Killip & Smith 22099* (NY). Cuzco: Oropeza Valley, Hacienda Guispicanchi, II–1929, *Herrera 2595b* (US), Cuzco without locality, 3000–3600 m, VII–1923, *Herrera s.n.* (US). Puno: San Antonio de Esquilache, 15000 ft, *Stafford 741* (F); near Nuñoa, 3900–4000 m, 10–III–1965, *Vargas 16237* (US). BOLIVIA. La Paz: La Fabulosa, 15000 ft, 26–IV–1950, *Brooke 6301 & 6301 a* (F, NY).

In his treatment of the *Compositae* in the *Chloris Andina*, Weddell described most of the forms involved in the *Perezia* complex except *P. pinnatifida* which had been circumscribed forty years earlier by Humboldt and Bonpland. Although Weddell's type specimens are quite distinct, evidence from collections now available suggests that he actually described hybrids in some cases and clinal extremes in others.

If only the type specimens are considered, it is immediately apparent that *Perezia coerulescens* and *P. nivalis* of Weddell are the same species. The slight differences between them are in the spininess of the leaves and the outer bracts, and the width of the basal leaves. *Perezia coerulescens* has narrower, more dissected, spinier leaves than *P. nivalis*. However, one specimen of *P. coerulescens* from Bolivia cited by Weddell is indistinguishable from the type of *P. nivalis*.

Two other taxa were later described which also, without doubt, fall within the variation of *Perezia coerulescens*. A variety of the species described as *P. coerulescens* var. *amplibracteata*, is identical with the type of *P. coerulescens* except that the flower color is orange rather than blue. Another proposed species, *P. nitidifolia* Koster is also practically identical with one of Weddell's original specimens of *P. coerulescens* and is also accordingly placed in synonymy with the latter.

Part of the confusion in the application of the name *Perezia coerulescens* is possibly due to an illustration in Weberbauer's book (1945, Fig. 25). Apparently, many taxonomists who had not seen the type of *P. coerulescens* used this picture for identi-

fication of specimens. Unfortunately, the plant depicted was probably a hybrid between *P. coerulescens* and *P. pinnatifida*.

Three other species described by Weddell, *Perezia integrifolia*, *P. violaceae*, and *P. cirsiifolia* are more similar to one another than to the types of *P. coerulescens* and *P. nivalis*, but are considered here to fall within the range of *P. coerulescens*. The type of *P. integrifolia* (a very poor specimen) is similar to that of *P. nivalis*, and is transitional in morphology to the forms described as *P. cirsiifolia* and *P. violaceae*. The type of *P. cirsiifolia* is a bizarre specimen and again, could be a hybrid between *P. coerulescens* and *P. pinnatifida*. The only plants I have seen which approach the type in morphology are from a collection by Tovar from Huancavelica, Perú which also includes specimens showing a combination of characters that suggests introgression from *P. pinnatifida* into *P. coerulescens*. The type specimen of *P. violaceae* is similar to plants of *P. coerulescens* found in Argentina and treated as *P. burkartii* by Cabrera.

A transition from the spinier type *(Perezia coerulescens sensu stricto)* to the broader leafed type *(P. violaceae–P. burkartii)* can be seen if a large series of specimens from central Perú to Argentina is examined. From Huanuco to Cuzco (Perú), almost all examples have dissected, spiny basal leaves and spiny outer bracts. However, starting at Huancavelica, the heads become progressively broader and the bracts wider and less spiny. A mixture of forms can be found from Puno (Perú) across Bolivia. Three large collections from Bolivia (the *Bang 1217* from the Bolivian Plateau; the *Fiebrig 3172* from Calderillo; and the *Steinbach* 9827 from San Benito) all show combinations of characters associated with presumed different species. The three collections are similar in head size and outer bract shape and differ only in leaf size and shape. Since there is a trend from dissected to entire leaves discernible from mid-Perú through Bolivia, it seems unreasonable to use leaf margin alone as a basis for separating the forms.

All of the plants from southern Bolivia and northern Argentina appear to have spineless, non-dissected leaves although the leaf margins are sometimes ciliate or lobed.

Two other species are considered here to belong with *Perezia coerulescens* in its species group. Both of them, *P. pygmaea* and *P. pinnatifida*, appear to be very closely related to *P. coerulescens* and there is evidence that *P. coerulescens* and *P. pinnatifida*

hybridize in certain localities (see above). I have kept the two species separate for several reasons despite the fact that some intermediate specimens can be found. First, the habitats of the two taxa differ: *P. coerulescens* grows in wet, short grasslands; and *P. pinnatifida* in rocky, drier environments. Hybrids are probably formed where the habitats of the two species overlap or where there has been disturbance of the pristine habitats by man.

Second, *Perezia coerulescens* differs morphologically from *P. pinnatifida* by its flat, rather than inrolled, basal leaves and strigose rather than pilose achenes. The outer bracts of *P. pinnatifida* are as long as the inner bracts and broad at the apex; those of *P. coerulescens* are shorter than the inner and lanceolate in outline. (Compare PLATE 2–1 with 2–3.) Plants of *P. pinnatifida* are densely hispid whereas those of *P. coerulescens* are usually much less pubescent.

There are also several morphological similarities between *Perezia coerulescens* and *P. pygmaea*. In fact, the two taxa may be conspecific but there is difference enough to warrant a separation of the species until further work can be done. *P. pygmaea* appears to have consistently only four or five basal leaves each of which have no more than four or five lobes on either side of the midrib. Both *P. coerulescens* and *P. pinnatifida* have larger, more numerous leaves with at least ten segments, although there are some populations of *P. coerulescens* with practically entire leaves. *P. pygmaea* also has comparatively fewer outer bracts than *P. coerulescens*, and pilose achenes. (Compare PLATE 2–1 with 2–2.)

26. PEREZIA PINNATIFIDA (H. & B.) Wedd.

Chaetanthera pinnatifida Humboldt & Bonpland, Pl. Aequin. **2**:170. Plate 136. 1809. Type: ECUADOR. Cotopaxí. Cotopaxí, *Humboldt*. (Since the type of this species was not found in the Humboldt Herbarium at Paris, it is believed to have been destroyed in Berlin.) Lectotype: Illustration in *Plantae Aequinoctialis*. Plate 136.

Homanthis pinnatifidus (H. & B.) Humboldt, Bonpland & Knuth, Nov. Gen. Sp. Plant. **4**:308. 1820 (quarto edition).

Homoeanthus pinnatifidus (H. & B.) Sprengel, Sys. Veg. **3**:503. 1826.

Homoianthus pinnatifidus (H. & B.) D. Don, Trans. Linn. Soc. I. **16**:209. 1830.

Clarionea pinnatifida (H. & B.) de Candolle, Prodr. **7**:62. 1838.

Perezia pinnatifida (H. & B.) Weddell, Chloris Andina **1**:40. 1855.

Compact rosette plant 2–12 cm tall. Rootstocks rhizomatous. Flowering stems hidden in the foliage, bearing 3 or 4 sheathing, lyrate to lanceolate,

obtuse and dentate stem leaves. Basal leaves numerous in a full rosette, lyrate in outline, obtuse, deeply dentate with the segments often conduplicate and with short cilia along the margins which tends to "seal" the fold; leaf bases attenuate or flaring, membranous; leaves 7–22 mm wide, 5–16 cm long; surface usually covered with dense glandular trichomes. Capitula narrowly campanulate, 13–30 mm wide, 16–31 mm long; upright. Involucres narrowly turbinate, 12–30 mm wide, 14–26 mm long, composed of 3–6 rows of bracts. Outer bracts pandurate in outline, obscuring the inner bracts, acute to obtuse, dentate at the apex, 4–10 mm wide, 9–23 mm long, densely glandularly pubescent. Inner bracts lanceolate, acute, 2–6 mm wide, 12–24 mm long, slightly pubescent at the apex. Pappus setose, brown, 1–1.7 cm long. Florets brownish, yellow, white or "pinkish-blue;" 1.5–4.3 cm long with ligules 5–12 mm; 14–48 per capitulum. Achenes with glandular trichomes; 2–5 mm long. Receptacle glabrous.

Distribution: perhaps in Ecuador; in Perú at very high elevations south to northern Bolivia (Fig. 26–3). Altitudinal range 3000–5000 m. Flowers March to May (PLATE 2–3).

Representative specimens: PERU. Lima: Huarón, 12–VI–1922, *Macbride & Featherstone 1136* (GH); Río Blanco, 15000 ft, 20–25–III–1923, *Macbride & Featherstone 3031* (F, GH, US); Auquimarca, III–1947, *Peraldo 3280* (F); Valley of the Rimac, 4850 m, *Raube & Hirsch P 94* (NY). Junín: Yauli, 13500 ft, 25–V–1922, *Macbride & Featherstone 929* (F, GH, US); above Casapalca at Mina Frei, 30–V–1965, *Vuilleumier 259* (GH). Huancavelica: Huancavelica, Paso de Chonta, 4800–4900 m, 8–V–1955, *Tovar 2947* (GH); Pisco, Rio Pisco, 4600 m, 10–III–1957, *Raube & Hirsch P 399a* (NY). Puno: San Antonio de Esquilache, 16000 ft, *Stafford 719* (BM), 15000 ft, 9–III–1937, *Stafford 1280* (F, BM). BOLIVIA. La Paz: Apacheta de Chuchu, 13–IV–1860, *Mandon 27* (P); Larecaja, vicinity of Sorata, between Pongo and Amlaya, 3600 m, 9–IV–1857, *Mandon 20* (GH, NY, P, US).

Perezia pinnatifida is the second member of the *P. coerulescens* complex. The species was described originally by Humboldt and Bonpland from an Ecuadorian specimen but it has not been reported since from that country. The habitat of *P. pinnatifida* is rocky outcrops at very high elevations, where individual plants nestle with their heads hidden in the basal rosette (PLATE 2–3). This characteristic aspect and the broad, long outer bracts make *P. pinnatifida* a rather easily recognized species.

The confusion which has sometimes arisen in the identification of some specimens is apparently due to the presence of hybrids between *Perezia pinnatifida* and *P. coerulescens*. Some intermediate specimens have basal leaves like those associated with *P. pinnatifida*, but have strigose (rather than pilose) achenes and glabrous foliage. (See PLATE 2–1 and 2–3.) Other specimens like *P. coerulescens* in aspect have the pubescence characteristic of *P. pinnatifida*. Both species occur in all areas from which I have seen intermediate specimens. Putative hybrids have not been reported from Argentina where only one of the two species grows.

27. Perezia pygmaea Wedd.

Perezia pygmaea Weddell, Chloris Andina 1:40. 1855. Type: BOLIVIA. La Paz: Ravine of Chuquiaguillo, near La Paz, 1851, *Weddell s.n.* (P).

Tiny rosette plants 2–3 cm tall with a thick rhizomatous rootstock. Flowering stems slight striated, bearing 1–4 sheathing stem leaves which are scarious or chartaceous. Basal leaves 5 or fewer, lyrate in outline, obtuse, with up to 7 rounded marginal lobes, of which the terminal lobe is the largest; leaves with a tendency to become conduplicate upon drying; leaf bases attenuate, 4–8 mm wide, 15–40 mm long, glabrous or with some scattered trichomes. Capitula one per flowering stem, not more than two per plant, narrowly campanulate, 9–17 mm wide, 15–20 mm long; upright. Involucre turbinate due to the sheathing of the outer bracts. Outer bracts ovate, acute, entire, or very slightly dentate at the apex; 2–5 mm wide, 7–15 mm long, glabrous, broadly scarious. Inner bracts longer than the outer, lanceolate, mucronate, 2–5 mm wide, 10–14 mm long, glabrous, scarious on the edges. Pappus setose, brown, 8–15 mm long. Florets white, blue, or violet, 12–19 mm long with ligules 5–8 mm long; 8–15 per capitulum. Achenes 1–2 mm long, covered with sparse glandular trichomes. Receptacle glabrous.

Distribution: in the Andes from central Perú to Argentina (Fig. 26–2) at elevations from 4000–5000 m. Flowering from March to June. (PLATE 2–2).

Representative specimens: PERU. Junín: near Morococha, 4650 m, 24–IV–1942, *Grant 7576* (F, GH), Casapalca, 15500 ft, 21–V–1922, *Macbride & Featherstone 846* (F, GH, US), Mina Frei above Casapalca, 5000 m, 30–V–1965, *Vuilleumier 260* (GH). Huancavelica: Huancavelica, Tansiri cerca a Manta, 4400–4500 m, 31–III–1953, *Tovar 1152* (GH); Castrovirreina, near Laguna Choclococha, 4500–4600 m, 5–V–1955, *Tovar 2920* (GH). Puno: Melgar near Nuñoa, 3900–4000 m, 10–III–1965. *Vargas 16246* (US). BOLIVIA. La Paz: Cordillera de Coroico, 5000 m, 22–IV–1857, *Mandon 19* (F, GH, NY, P, US). ARGENTINA. Jujuy: Tres Cruces, Mina Aguilar, 4190 m, 22–IV–1965, *Vuilleumier 242* (GH).

Perezia pygmaea forms mats of several crowded plants closely appressed to the damp soil at snow line in the Andes of central Perú south to northern Argentina. This species is considered here to be a distinct member of the *P. coerulescens* complex, although it may ultimately be shown to be a high altitude (and consequently dwarfed) form of *P. coerulescens*. However, there is some evidence that it is a good species and should be maintained until further field work can be done.

At several localities (e.g., Junín, Perú and Ravine de Chuquiaguillo, Bolivia) both *Perezia pygmaea* and *P. coerulescens* have apparently been collected together, suggesting that two taxa are involved. In these areas plants of *P. coerulescens* have very dentate outer bracts and very deeply parted leaves and sympatric specimens of *P. pygmaea* have more entire bracts and basal leaves with only four or five lobes. (Compare PLATE 2–1 with 2–2.)

In some localities (such as in northern Argentina), specimens

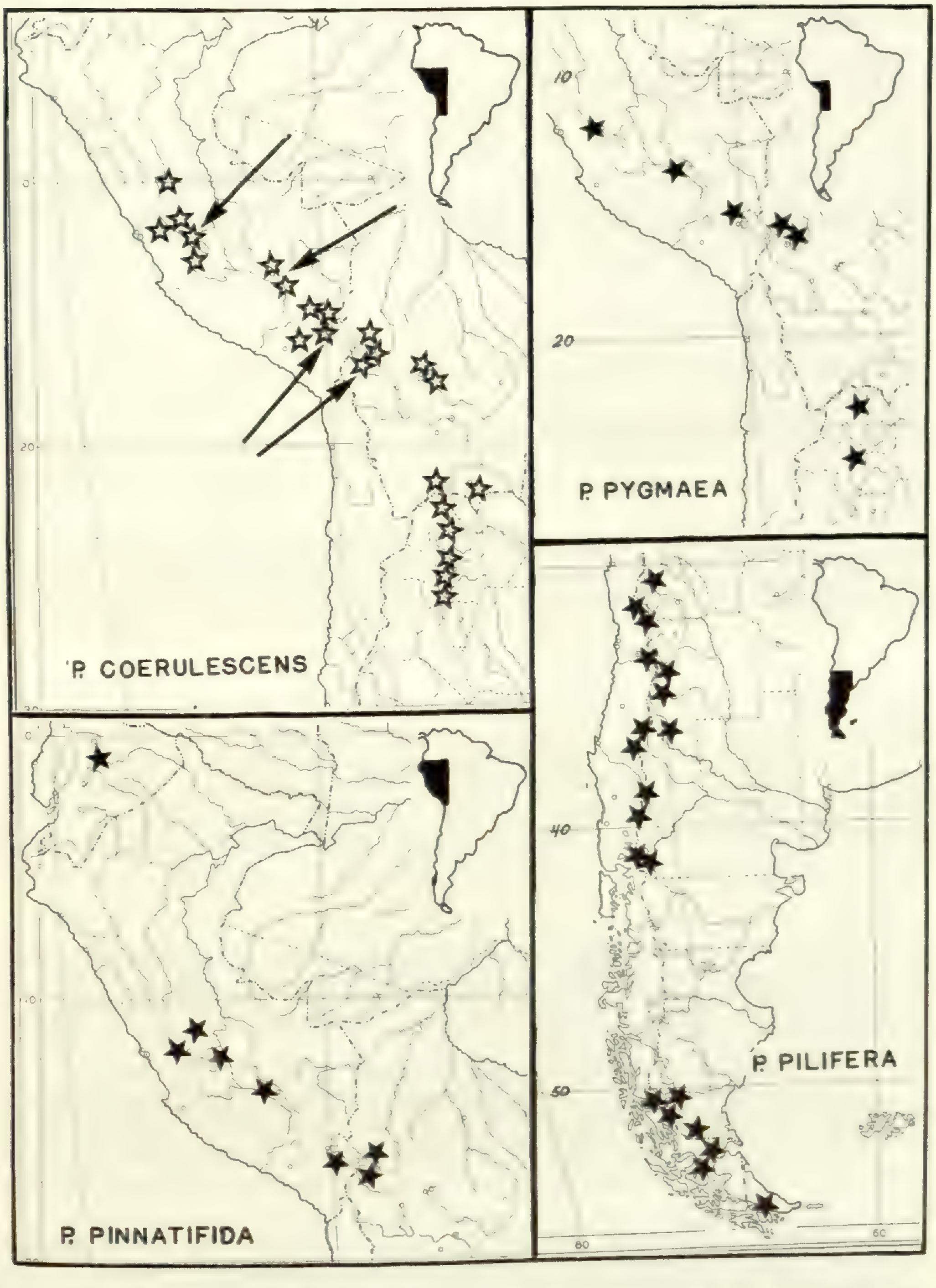


FIG. 26. Distribution of *Perezia coerulescens*, *P. pygmaea* and *P. pinnatifida*, the three members of the *P. coerulescens* group, and *P. pilifera*. Arrows indicate areas of possible hybridization between *P. coerulescns* and *P. pinnatifida*.

of *Perezia coerulescens* approach *P. pygmaea* in morphology except that they have strigose achenes.

The third member of the *Perezia coerulescens* group, *P. pinnatifida* is also known to grow sympatrically with *P. pygmaea* (i.e., Mina Frei in central Perú [Junín]) where they occupy separate habitats. Plants of *P. pinnatifida* prefer the rocky outcrops, whereas those of *P. pygmaea* grow on flat moist soil. Morphologically, the two species are also quite distinct. *Perezia pinnatifida* has comparatively large basal leaves which are inrolled and which hide the capitula. The basal leaves of *P. pygmaea* are appressed to the ground and the heads are held above them. The outer bracts of *P. pinnatifida* are long and thickened at the apex and obscure the inner, shorter, bracts. The outer bracts of *P. pygmaea* are shorter than the inner and are ovate in outline instead of elongate as in *P. pinnatifida*. (Compare PLATE 2–2 with 2–3.)

28. PEREZIA POEPPIGII Less.

Perezia poeppigii Lessing, Synop. Comp. 411. 1832. Type: CHILE. "Boreal Andes," *Poeppig s.n.* (P).

Clarionia virens D. Don. Trans. Linn. Soc. I. **16**:208. 1830. Lectotype: CHILE. Cordillera, *Cuming 238* (K). (Note: Don gave the type specimen as a Ruiz & Pavon collection, but Hooker & Arnott listed Cuming's specimen. I have not found a Ruiz & Pavon specimen of the species and agree with Hooker and Arnott that a mistake was made as it was in the case of *P. ciliaris*. I have, therefore, chosen the Cuming specimen as lectotype.

Perezia virens (D. Don) Hooker & Arnott, Comp. Bot. Mag. **1**:34. 1835.

Clarionema virens (D. Don) Philippi var. *humilis* Phil. Linnaea **33**:124. 1864. Type: CHILE. Coquimbo: Cordillera de Illapel (not seen).

Homoianthus pristiphyllus Remy in Gay, Fl. Chile **3**:419. 1849. Type: CHILE. Colchagua, II–1831, *Gay 310* (P).

Perezia pristiphylla (Remy) Weddell, Chloris Andina **1**:37. 1855.

Clarionea caulescens Phil., Anal. Univ. Chile **87**:301. 1894. Type: CHILE. Colchagua: Cordillera de San Fernando, I–1884, *Herth s.n.* (SGO).

Homoeanthus remyanus Phil., Anal. Univ. Chile **87**:310. 1894. Type: CHILE. O'Higgins: Cordillera de Popeta, Las Lenas, I–1887, *Philippi 2252* (SGO, Isotype LP).

Homoeanthus brevicaulis Phil., Anal. Univ. Chile **87**:309. 1894. Type: CHILE. O'Higgins: Cordillera de Popeta, *Philippi s.n.* (SGO).

Clarionea nana Phil. Anal. Univ. Chile **87**:303. 1894. Type: CHILE. Coquimbo: Illapel, Las Mallacas, I–1888, *no collector* (SGO).

Small, bright, rosette perennial herb 4–13 cm tall. Stems woody at the base, slightly pubescent under the capitula, green, bearing 1–3 leaves. Stem leaves scattered up the stem, lanceolate to slightly spathulate in outline, acute, clasping, spiny along the margins; surface with glandular punctate dots. Basal leaves few, oblanceolate to lanceolate in outline, obtuse to acute, edges with deep oblong teeth or scalloped, edges of segments with short cilia or spines; leaves attenuate at the base; width 3–17 mm, length 13–90

mm; surface with glandular punctate dots or rarely with a few glandular trichomes. Flowering stems with one or two capitula. Individual heads turbinate, 22–40 mm wide, 22–30 mm long; upright. Involucres turbinate, 15–35 mm wide, 15–27 mm long; composed of 4–5 rows of bracts. Outer bracts lanceolate, acute, slightly spiny, 2–4 mm wide, 6–14 mm long; surface with glandular punctate dots or a few scattered glandular trichomes; scarious along the margins. Inner bracts lanceolate, acute, entire, 2–4 mm wide, 9–21 mm long, rigid, covered with glandular punctate dots; scarious along the margins. Pappus setose, beige, 13–19 mm long. Florets cream, yellow, or red; outer florets 21–29 mm long with ligules 6–12 mm long; 11–14 florets per capitulum. Immature ovaries 2–4 mm long, covered with glandular trichomes and/or scattered double hairs. Mature achenes up to 5 mm long. Receptacle with short tufts of gold trichomes around the point of achene attachment.

Distribution: limited to the Chilean side of the Andes from northern Coquimbo to mid-Colchagua at elevations of 1700–3200 m (Fig. 27–2). Flowering season from December to March.

Representative specimens: CHILE. Coquimbo: Cordillera de Ovalle, 3131 m, I–1837, *Gay 425* (P); Dpto. Illapel, Vega Escondida 2640 m, 21–XII–1936, *Morrison 16966* (GH). Aconcagua: Dpto. Quillota, Cerro Caquis, 15 km east of Melón, 1750–2040 m, 14–XII–1933, *Morrison 16899* (GH, LIL); 6 km before Portillo, 2450 m, 16–I–1964, *Marticorena & Matthei 616* (CONC), Portillo, 2870 m, 6–III–1954, *Ricardi 2846* (CONC). Santiago: Alhué, Monte Cantillana, 2–I–1939, *Barros 2025* (LP, SI); Río Yeso, Laguna Negra, 13–I–1945, *Biese 930* (LIL), Perez Caldera, 2600 m, 17–I–1964, *Marticorena & Matthei 645* (CONC). Colchagua: San Fernando, Vegas del Flaco, 1250 m, 21–I–1930, *Montero 1757* (GH).

Perezia poeppigii is limited in distribution to the area south of the Atacama desert and north of the *Nothofagus* forest (Fig. 27–2) as is true of many other endemic Chilean angiosperms. *Perezia poeppigii* is the only species of *Perezia* to have this geographical pattern, although *P. carthamoides* has a series of distinctive populations in the same area. The habitat of *P. poeppigii* seems to be rocky crevices in the scrubland or monte of the longitudinal valley of central Chile.

Although the range of *Perezia poeppigii* is fairly restricted, there is some geographical variation in morphology from north to south. In the central part of the province of Santiago at Alhué (Monte Cantillana) and south to Colchagua, plants have leaves which are scalloped, spiny and not as dissected as those of other populations. Plants from this area (described as *Homoianthus prystiphyllus* Remy) are also more elongate than those from other regions.

Philippi described four other species considered here to be geographical races of *Perezia poeppigii*. Three of the four (*Homoeanthus remyanus, H. brevicaulis,* and *Clarionea caulescens*) were

described from central Chilean specimens and belong to the same geographical race as Remy's *Homoianthus prystiphyllus*. Philippi's fourth species, *Clarionea nana*, was described from a northern Chile specimen and is merely a small plant of the form originally described as *P. poeppigii*.

On morphological grounds, it is evident that *Perezia poeppigii* is part of the *P. recurvata* species group and is, in fact, probably similar to the stock which gave rise to both *P. linearis* and *P. recurvata*. A logical sequence of morphological specialization leading to the needle-like, recurved leaf of *P. recurvata* would seemingly begin with a broad, flat laminar type of leaf, progress to a linear, flat leaf, and finally, by inrolling of the margins, produce the type now found in *P. recurvata*. Such a sequence is visible from *P. poeppigii* through *P. linearis* to *P. recurvata*. These three species also share the characters of a similar achenial trichome type (Fig. 3–2, Table 3), very turbinate heads, and stiff, lanceolate involucral bracts.

The only two species with which *Perezia poeppigii* might be confused are *P. linearis* and *P. carthamoides*. Plants of *P. poeppigii* with rather entire leaf margins approach *P. linearis* in aspect, but can be simply distinguished because the leaves are larger and do not have the dense even cilia along the margins which is characteristic of *P. linearis*. Also, the florets of *P. linearis* are always blue whereas those of *P. poeppigii*, although sometimes blue, are more frequently cream, yellow, or red.

Small specimens of *Perezia carthamoides* with reduced basal leaves have sometimes been misidentified as *P. poeppigii* but the former can always be distinguished from the latter because of its broadly hemispherical, rather than turbinate, capitula, and its broadly scarious ovate bracts. In the province of Santiago, Chile, where the two species are sympatric, *P. carthamoides* has upright panicles of several heads whereas plants of *P. poeppigii* have monocephalous (rarely dicephalous) flowering stems.

29. Perezia linearis Less.

Perezia linearis Lessing, Synop. Comp. 412. 1832. Type: CHILE. Bío Bío: Austral Andes near Antuco, *Poeppig 767* (P, Isotypes NY).

Homoianthus linearis (Less.) de Candolle, Prodr. 7:64. 1838.

Homoeanthus rigidus Philippi, Linnaea 28:719. 1858. Type: CHILE. Linares: Cordillera de Linares, II–1856, *Germain s.n.* (SGO).

Homoianthus pectinellus Gandoger, Bull. Soc. Bot. Fr. 18:45 (65 of

total series, 18 of Ser. 4). 1918. Type: ARGENTINA. Patagonian Andes, 1100 m, *Buchtein* (type not seen).

A small species tending to form loose mats by branching at the base and creeping over the ground. Plants 4–31 cm tall, but prostrate if longer than 15 cm. Flowering stems densely pubescent with glandular trichomes; bearing 1–15 clasping, lanceolate, acute, and densely ciliate stem leaves. Each stem leaf up to 3 mm wide and 2.5 cm long. Basal leaves in clusters forming small rosettes, individual leaves linear but slightly spathulate, mucronate, and densely ciliate along the margins; leaf edges never recurved, rather frequently conduplicate upon drying; 1–4 mm wide, 1.2–3.8 cm long; glabrous or with glandular punctate dots. Capitula one per flowering stem, funnel shaped, 2–4.4 cm wide, 2–3.2 cm long; upright. Involucre turbinate, 6–40 mm wide, 1.2–3.3 cm long; composed of 3–6 rows of bracts. Outer bracts lanceolate, acute, ciliate, 1–4 mm wide, 5–19 mm long; usually glabrous but sometimes with a few scattered glandular trichomes; occasionally red-tipped and with dark green centers; edges scarious. Inner bracts lanceolate, acute, slightly ciliate, 1–9 mm wide, 9–24 mm long, usually with long glandular trichomes at the apex; slightly scarious along the margins. Pappus setose, beige, or white, in a few cases with a pinkish tinge, 1–2 cm long, full. Florets blue or white, outer florets 1.3–3.3 cm long with ligules 6–13 mm long; about 8–16 per capitulum. Ovaries 1–4 mm long with scattered double hairs. Mature achenes to 4 mm long, less pubescent than the ovaries. Receptacle covered with tufts of golden trichomes.

Distribution: in Argentina in the Andes of Neuquén south to the region of Lago Argentino. In Chile all along the Cordillera from Concepción to Aysén (Fig. 27–3). Altitudinal range from 600–1600 m. Flowering January to March.

Representative specimens: ARGENTINA. Neuquén: Parque Nacional Nahuel Huapí, subido al refugio Cerro Colorado, 1200 m, 24–II–1951, *Diem 1875* (SI). Río Negro: Parque Nacional Nahuel Huapí, Cerro Belvedere, 21–III–1934, *Spegazzini 107* (GH), Cerro Goye, 14–II–1965, *Vuilleumier 203* (GH); Río Casa de Piedra, 1100 m, 10–I–1929, *Cordoni 252* (US); Lago Hess, 10–I–1945, *Meyer 8120* (A). Chubut: Río Frias, Putrachoique, I–1899, *Illin s.n.* (BAB); Río Pico, *Roth s.n.* (NY). Santa Cruz: Lago Argentino, West of the Santa Cruz River, 1907–1908, *Furlong 159* (GH); Peninsula Avellaneda, 14–II–1914, *Hicken & Hauman 934* (SI); Sierra Buenos Aires, 5–III–1914, *Hicken & Hauman 961* (SI); Lago Viedma, I–1916, *Wittes 49* (NY). CHILE. Concepción: Province de Concepción, 1839, *Gay 284* (P). Colchagua: Cajón de Azufre, II–1831, *Gay 946* (P). Maule: Cordillera de Maule, 1885, *Germain s.n.* (P). Linares: Cordillera de Linaris, 2–II–1939, *Barros 2004* (SI). Bío Bío: camino de Icalma a Liucura cerca la confluencia del Chanco Loco con el Bío Bío, 1000 m, 16–I–1947, *Pfister s.n.* (CONC). Malleco: Curacautin, 19–I–1928, *Joseph 4884* (US); Lonquimay, II–1930, *Gunkel 1387* (GH); confluencia del Rahué con el Bío Bío, 8–I–1947, *Pfister s.n.* (CONC). Cautin: Volcan Llaima, 1000 m, II–1927, *Werdermann 1217* (F, GH, NY, SI, US); Department of Victoria, road from Termas de Tolhuaca to Laguna de Malleco, 950–1100 m, 10–III–1939, *Morrison & Wagenknecht 17464* (GH). Aysén: Estero Las Mulas, afluente del Río Ibanez, 2–II–1962, *Behn s.n.* (CONC); region del Lago Buenos Aires, Valle León, cerca del Río Meliquina, 3–II–1939, *Rentzell s.n.* (SI).

In clearings in the higher parts of the *Nothofagus* forest and along the edges of the forest in Patagonia, *Perezia linearis* is a

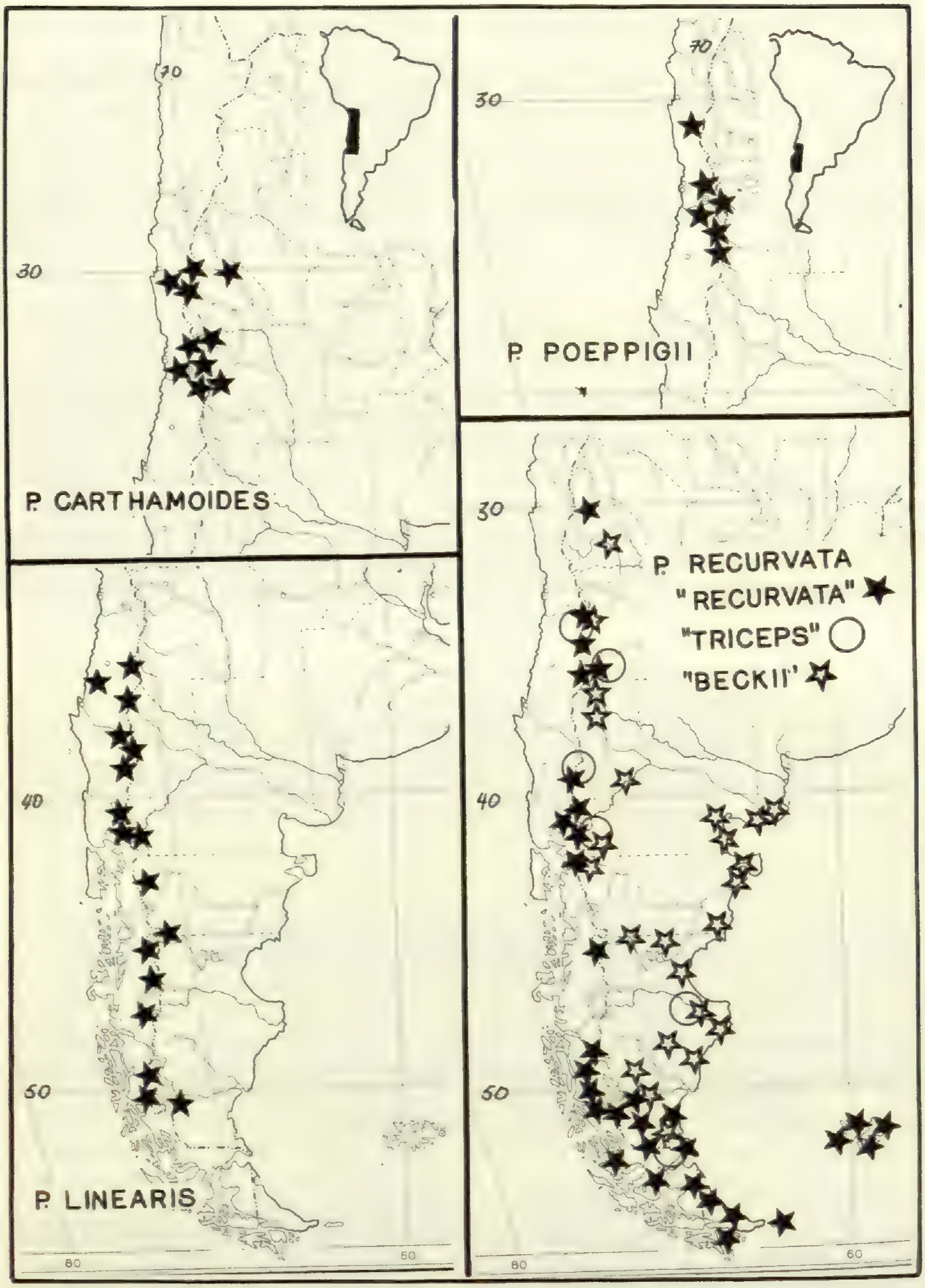


FIG. 27. Distribution of *Perezia carthamoides* of the *P. pungens* group and the three members of the *P. recurvata* species group: *P. poeppigii*, *P. linearis*, and *P. recurvata*. FIG. 27–4 shows the distribution of 'the three phenotypes present in *P. recurvata*. See also FIG. 28 and text.

fairly common species (Fig. 27–3). It seems to prefer well drained soils and some sun, but does not occur to any extent on the true Patagonian steppe, nor in the high puna well above timberline. Thomasson (1959) reported the species growing with *Fuschia magellanica (Onagraceae)* and *Calceolaria tenella (Scrophulariaceae)* in a more moist habitat than the localities in which I have seen the species. The species varies little geographically despite its extended latitudinal range.

It is possible that *Perezia linearis* is actually one of the polymorphic forms of *P. recurvata* because plants of the two species from the same locality are exceedingly similar except in the character of recurving of the leaf. Mixed collections of the two species are common from the areas of sympatry. The only constant difference between the two species is that *P. linearis* has flat leaves of thinnish texture with a dense even row of cilia along the margins and bracts with evenly ciliate margins (Fig. 29–a). *Perezia recurvata* has thick leaves which are strongly recurved and have spines on pseudomargins and bract edges (Fig. 29, b to r). No specimen of *P. linearis* has been seen which has leaves that tend to recurve. In fact, the leaves of *P. linearis* often become conduplicate upon drying. Furthermore, no individuals have been found which have a trace of spines or long trichomes on the upper surface of the leaf blade.

There also appears to be a habitat separation of the two species. *Perezia linearis* grows within the *Nothofagus* forest and along the forest edges. *P. recurvata* is a puna and steppe species.

Because of the consistency of the leaf characters and the ecological separation, the two are retained here as distinct taxa. Further investigations will show whether or not this interpretation is correct. Undoubtedly, the two are very closely related and were derived from a common stock. The ancestral form common to the two probably had flat leaves much like those of *Perezia linearis.*

30. Perezia recurvata (Vahl) Less.

Perdicium recurvatum Vahl, Skriv. Nat. Selsk. Kiøb. **1**:13. Tab. 7. 1790. Type: CHILE. Magellanes: Straits of Magellan, *Commerson s.n.* (C, Isotype P, CONC).

Chaetanthera recurvata (Vahl) Sprengel, Sys. Veg. **3**:503. 1826.

Perezia recurvata (Vahl) Lessing, Linnaea **5**:21. 1830.

Clarionia recurvata (Vahl) D. Don, Trans. Linn. Soc. I. **16**:206. 1830.

Perezia recurvata (Vahl) Less. var. *sessilis* Dusen, Arch. Bot. Stockh. 7(2):46. Taf. 6(4). 1908. Type: ARGENTINA. Chubut: Colonia San Martin, 750 m, *Hogberg s.n.* (type not seen).

Homoianthus echinulatus Cassini, Dict. Sci. Nat. 38:458. 1825. Type: CHILE. In insulis Maclovanis (Falkland Islands), *d'Urville & Gaudichaud s.n.* (P).

Perezia doniana Lessing, Synop. Comp. 412. 1832. Type: CHILE. without locality, *Ruiz & Pavon s.n.* (type not seen).

Homoianthus donianus (Less.) Remy in Gay, Fl. Chile 3:422. 1849.

Perezia reflexa Meyen, Reise um die Erde 1:311. 1834. Type: CHILE. Colchagua: Cordillera de San Fernando, 31–I–1833, *Meyen s.n.* (type destroyed at Berlin, Photo 16086, GH).

Homoianthus inermis Meyen & Walpers, Nov. Acta Acad. Leop.-Carol. 19 (Supp. 1):290. 1843. An illegitimate name for the same specimen described as *P. reflexa* by Meyen in 1834.

Perezia beckii Hooker & Arnott, Comp. Bot. Mag. 1:34. 1835. Type: ARGENTINA. Patagonia, *Dr. Eights 62* (K).

Homoianthus pectinatus Philippi, Anal. Univ. Chile 2:396. 1862. Linnaea 33:124. 1864. Type: ARGENTINA. Mendoza: Portillo, 1861–1862, *Diaz s.n.* (SGO).

Perezia pectinata (Phil.) Reiche, Anal. Univ. Chile 116:437. 1905. Fl. Chile 4:455. 1905.

Homoeanthus triceps Philippi, Anal. Univ. Chile 87:307. 1894. Type: CHILE. Bío Bío: Guaieltué, II–1887, *Rahmer s.n.* (SGO, Isotype LP).

Perezia triceps (Phil.) Reiche, Anal Univ. Chile 116:431. 1905. Fl. Chile 4:449. 1905.

Perezia patagonica Spegazzini, Rev. Fac. Agron. Vet. 3 (30–31):540. 1897. Type: ARGENTINA. Santa Cruz, 1882, *Spegazzini s.n.* (LP).

Perezia patagonica Speg. var. *intermedia* Speg., Rev. Fac. Agron. Vet. 3(32–33):615. 1897. Type: ARGENTINA. Chubut: without locality, 1889, *Moyano s.n.* (LP).

Perezia flavescens Dusén, Arch. Bot. Stockh. 7(2):46. 1908. Type: ARGENTINA. Puerto San José, 11–XII–1904, *Dusén* 5355 (Type destroyed at Berlin, Photo GH, LIL; Isotype HBG).

Homoianthus patagonicus Gandoger, Bull. Soc. Bot. Fr. 18(Ser. 4):45. 1918. Non *Perezia patagonica* Spegazzini. Type: ARGENTINA. Río Negro: Bariloche, 1100 m, 19–II–1905, *Buchtein 1339* (HBG, Isotypes GH, US). An illegitimate name since it is a later homonym of *Perezia patagonica* Speg.

Small mat forming plants extremely woody and branched at the base and with decumbent or upright stems; 4–30 cm tall. Stems terete, frequently with a few glandular trichomes below the head; sometimes streaked with red. Stem leaves actually a continuation of the basal leaves up the stem; decreasing in size as they approach the capitulum; lanceolate or linear in outline, acute or mucronate, margins recurved or not, either the pseudomargins or the true margins sometimes with white spines. Stem leaves usually glabrous, but sometimes with scattered glandular trichomes. Basal leaves most frequently crowded at the base of the stem; linear in outline, mucronate, the margins always recurved and the pseudomargins smooth, with small soft spines, or with a single or double row of stiff long white spines; leaf base flaring and clasping; 1–5 mm wide, 7–37 mm long; surface smooth, glabrous, or in some cases with furrows running at right angles to the midrib. Capitula 1–3 per flowering stem. Flowering stems axillary, several present per plant. Individual capitula 1.5–2.5 cm wide, 9–25 mm long, upright. Involucre hemispherical or turbinate, 9–19 mm wide, 10–25 mm long; composed of

3–9 rows of bracts. Outer bracts ovate, mucronate, margins ciliate, or with long stiff white spines, 1–4 mm wide, 3–10 mm long, sometimes glabrous but usually with glandular trichomes scattered along the surface, scarious along the edges, sometimes reddish at the apex. Inner bracts lanceolate, acute, entire, 1–5 mm wide, 10–27 mm long, usually with a few glandular trichomes at the apex, sometimes red tipped. Pappus setose, 9–20 mm long, white, brown or pinkish. Florets blue, white, cream, or yellow, outer florets 1.7–3.4 cm long with ligules 6–11 mm long; 8–20 per capitulum. Immature achenes with a few scattered double hairs especially at the apex, or with double hairs mixed with glandular trichomes, or rarely glabrous; 2–5 mm long. Mature achenes 5 mm long, less pubescent than the ovaries. Receptacle with rings of red or tawny trichomes around the point of an achene attachment.

Chromosome number: $2n=24$ (or 26).

Distribution: from Colchagua in Chile south along the Andes through Tierra del Fuego. In Argentina south from Mendoza to Tierra del Fuego and east to the Atlantic Ocean. Also found on the Falkland Islands (Fig. 27–4). Flowering October to March (PLATE 2–4).

Representative specimens: ARGENTINA. San Juan: Department of Inglesia, Cordillera de Colanquil, *Brackenbush s.n.* (CORD). Mendoza: Paso Cruz, 3000 m, *O. Kuntze 103* (US), *192* (NY, US); Valle de Calmu-có, 14–II–1940, *Burkart, Troncoso & Nicora s.n.* (SI); Malalluce, Cerro Miraus, cerca de Ruta 40, 18–I–1956, *Castellanos 3514* (LIL); Department of Beltrán, entre Rio Grande y Arroya Calqueque, 30–I–1888, *Kurtz s.n.* (CORD). Buenos Aires: Viedma, 15–II–1947, *Scolnik 410* (LIL); Secus River, II–1909, *Silvestri s.n.* (BAB); Rio Santa Cruz, II–1900, *Burmeister s.n.* (BAB); 20 leguas oeste de Santa Cruz, 31–I–1914, *Hicken & Hauman 481* (SI); Puerto Deseado, 13–I–1914, *Hicken & Hauman 167* (SI); Monte León, 27–I–1914, *Hicken & Hauman 1019* (SI); 50 km north of San Julian, 30–XII–1938, *Eyerdam, Beetle & Grondona 23957* (F, GH); 24 km south of Piedrabuena, 1–I–1939, *Eyerdam, Beetle & Grondona 24019* (GH); limite internacional hito XIX, 11–III–1921, *Pastori 189* (SI); Tierra del Fuego, region del Río del Fuego, III–1902, *Holmber & Calcagnini 333* (BAB); Mision Río Grande, 4–III–1921, *Pastori 119* (SI); Isla de los Estados, 1902, *Rodriguez 28* (BAB). FALKLAND ISLANDS. Catherine Point, I–1867, *Cunningham s.n.* (GH); West Falkland Islands, Rocky Cove, II, *Vallentin s.n.* (K); East Falklands, Sparrow Cove, north of Point Stanley, I, *Sladen Fa 27/50* (BM). CHILE. Colchagua: San Fernando, Vegas del Flaco, 10–II–1955, *Ricardi 3224* (CONC). Curíco: Potero Grande, lomas grande, *Barros 7464* (LP). Talca: Laguna del Maule, 2200 m, I–1943, *Behn s.n.* (CONC). Valdivia: *Lechler 1181* (HBG). Aysén: Río Nireguao, Estancia Baños Nuevos, 700 m, 17–I–1939, *von Rentzell s.n.* (SI). Magellanes: Lago Arsutono, I–1900, *Prichard s.n.* (NY); Cerros de la Cueva del Mylodon, 13–I–1957, *Pfister & Ricardi s.n.* (CONC); Morro Chico, 9–I–1952, *Pfister & Ricardi s.n.* (CONC); Puerto Natales, 16–I–1933, *Jara s.n.* (CONC); Cerro Doratea, 5 km north of Puerto Natales, 8–I–1939, *Eyerdam, Beetle & Grondona 24191* (GH); Carmen de Patagones, 9–X–1937, *Miccio 45a* (LP); Orilla, norte del Río Negro, 10–IX–1874, *Berg 119* (LP). Neuquén: Chos Malal, 24–I–1964, *Boelcke 11116* (LP); Lago Traful, 17–I–1935, *Cabrera & Job 408* (LP); Volcan Tromen, Rahui Pass, 25–II–1888, *Kurtz 6146* (CORD); Lago Huechulafquen, 2–I–1945, *O'Donnell 2286* (LIL). Río Negro: Bariloche, base of Cerro Otto, 9–II–1965, *Vuilleumier 196* (GH); Pilcaniyeu, 20–II–1938, *Nicora 3658 & 3674* (SI); Arroya Verde, camino Verde, camino de San Antonio a Madryn, 14–II–1938, *Birabén & Birabén*

440 (LP). Chubut: Esquel, 20–I–1945, *Castellanos s.n.* (LIL); Comodoro Rividavia, 4–XI–1945, *O'Donnell 3425* (LIL); Puerto Piramides 8–I–1914, *Hicken & Hauman 201* (SI); Bolsón, 5–10–I–1901, *Illin 2* (HBG); Cholina, I–1900, *Illin* (BAB); La Sinica, 600 m, 21–I–1945, *Rohmeder 18* (A, LIL); Dpto. 16 de Octobre, Colonia Cushamen, 31–XII–1947, *Kraprovickas 3793* (BAB); Colonia Sarmiento, 24–III–1902, *Koslowsky s.n.* (BAB); Puerto San José, 11–XII–1904, *Dusén 5355* (HBG). Santa Cruz, south shore of Lago Argentino, 30 km west from the Santa Cruz River, 1907–1908, *Furlong 158* (GH); Cordillera Cristales, II, *James 219* (BM); Est. Fitzroy, 24–XII–1950, *Sleumer 1255* (LIL); Lago San Martín, Río Fosiles, 900 m, *Dusén s.n.* (LIL); Canadon León, 24–II–1936, *Birabén & Birabén 117* (LP); Lago Cardiel, 27–II–1936, *Birabén & Birabén 140* (LP); Río Gallegos, Killik Aike, *Brown 78* (NY); Tehuelches, ca. 300 m, 28–XI–1928, *Donat 63* (GH); Estancia Punta Delgada, Canadon Meric, 180 km, northeast of Puenta Arenas, 18–III–1964, *Moore 1038* (GH); Puerto Prat, 5–II–1904, *Hicken 25* (SI); Straits of Magellan, Elisabeth Island, I–1888, *Lee s.n.* (US); Ultima Esperanza, 5–I–1931, *Donat 388* (GH); Santa Catalina, 31–I–1936, *Behn s.n.* (CONC); Bahia Felipe, Estancia las Rosas, 23–I–1952, *Pfister s.n.* (CONC).

As is suggested by the large number of synonyms included here under *Perezia recurvata*, the species is polymorphic and widely distributed (Fig. 27–4, Fig. 28). Several rather consistent phenotypes recur throughout the range of the species. These phenotypes and several of the intermediate populations have been described as separate species, the separation of which was made on the

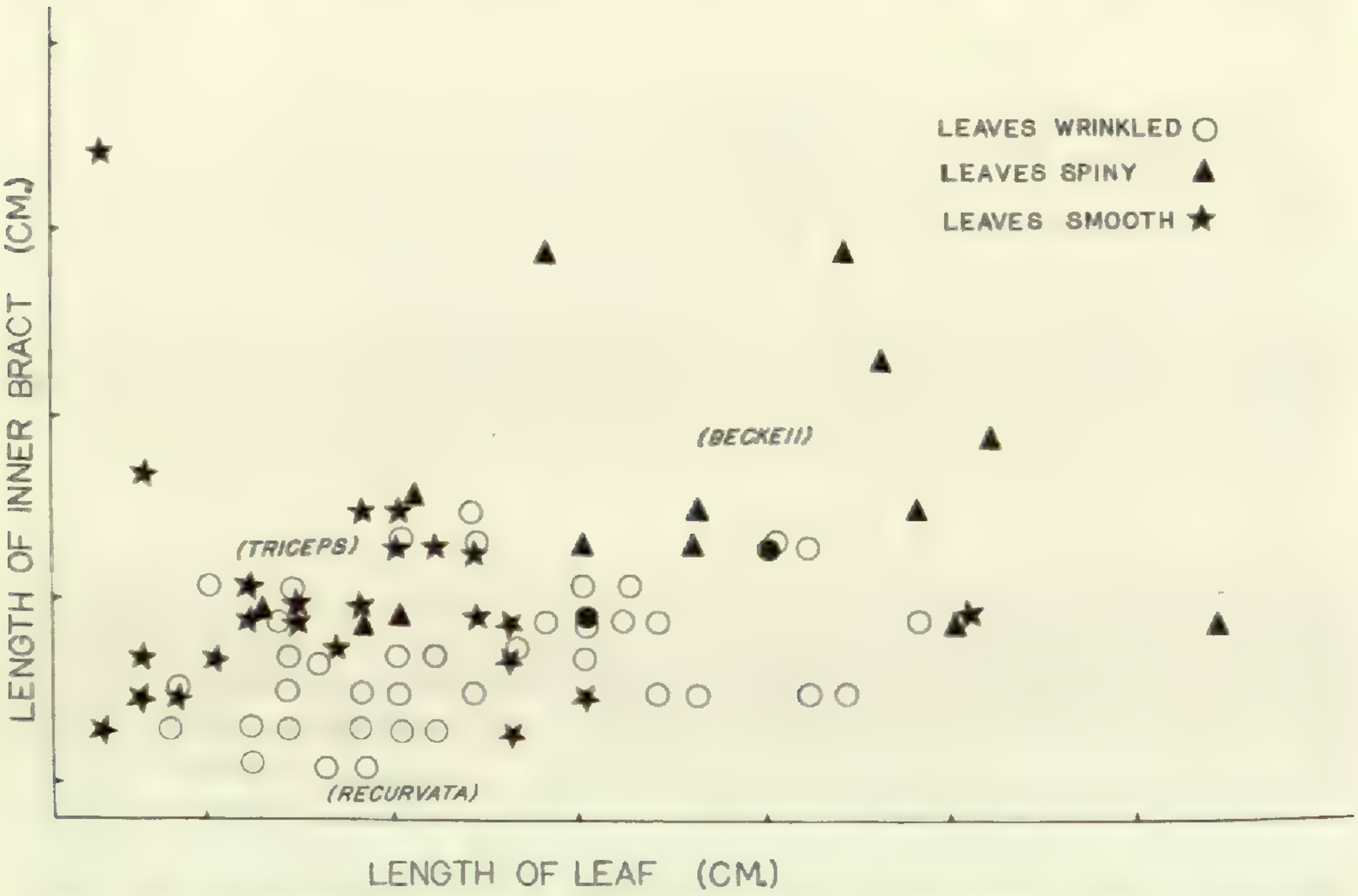


FIG. 28. Graph of leaf length *vs.* inner bract length of specimens of *Perezia recurvata* showing complete intergradation of these characters frequently used to separate the species into three distinct taxa. Each symbol represents one specimen.

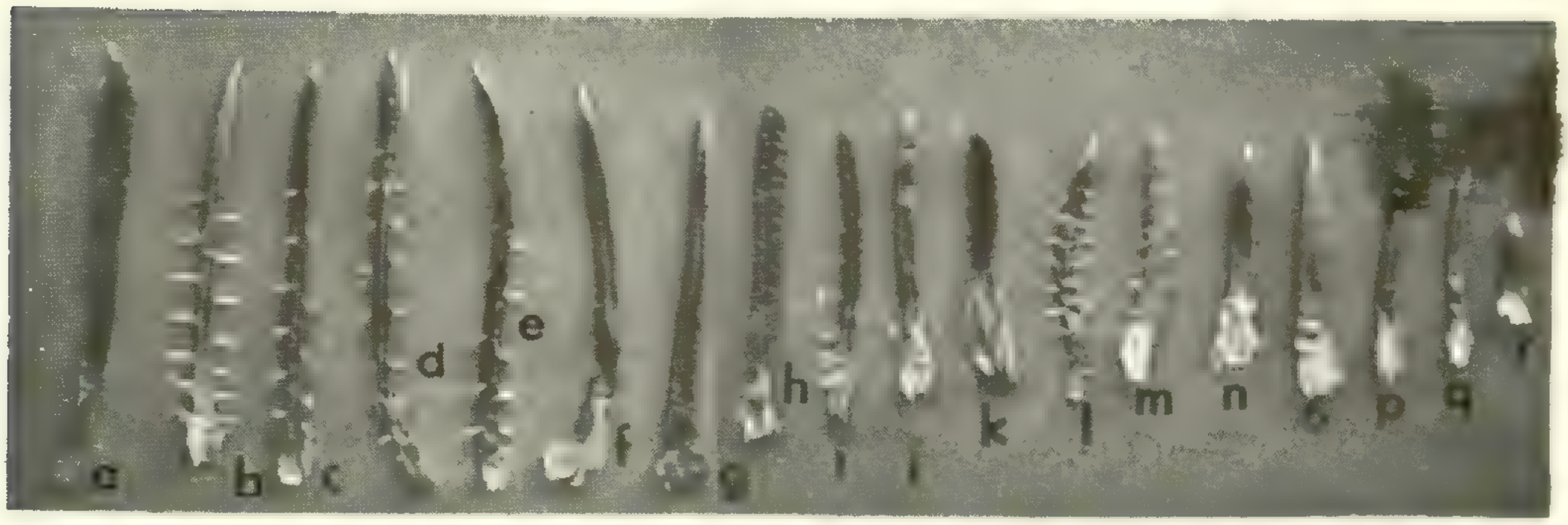


FIG. 29. Variation in the leaves of *Perezia recurvata*. Leaves *b*, *c*, *d*, *e* and *l* are the "beckii" phenotype. Leaves *f*, *g*, *j*, *o*, *p* and *q* are the "triceps" type. Representatives *h*, *i*, *k*, *m*, and *r* are considered the "recurvata" phenotype. Leaf *a* is from a plant of *P. linearis*. All natural size.

basis of the appearance of the leaf pseudomargins, the leaf surface, and the amount of curvature of the outer bracts. A brief discussion of the different phenotypes and their probable evolutionary history is included here to explain their inclusion into one species.

The phenotype originally described as *Perezia recurvata* has heads with rounded bases, upright involucral bracts, leaves which are transversely wrinkled and which have small spines along the edges (Fig. 29, leaves *h*, *i*, *k*, *m*, *r*). This "recurvata" form is common in southern and southeastern Patagonia and is found on the Falkland Islands.

Along the east coast of Patagonia and straying across the tableland is a form which has long stiff leaves without transverse wrinkles and much longer, stiffer white spines along the pseudomargins of the leaves and outer bracts than the eastern populations (Fig. 29, leaves *b*, *c*, *d*, *e*, *l*). The bracts of this form are always curved outward and the inner bracts are long and quite scarious. The pappus is usually pure white and the flowers tend to be yellow, rather than blue as they are in the "recurvata" form. This phenotype was described as *Perezia beckii* by Hooker & Arnott and is here referred to as the "beckii" phenotype.

Another type described by Philippi as *Perezia (Homoeanthus) triceps* has several heads (usually two or three) per flowering stem. Philippi described this form as having entirely smooth leaf edges, but Reiche (1905) stated that Philippi was mistaken and that the leaves usually have small spines along the pseudomargins. I agree with Reiche; in fact, the type specimen has small spines along the leaf edges, but they are hard to see with the naked eye.

Because Philippi described *Perezia triceps* as having smooth leaf edges, the name "triceps" has been applied to populations of *Perezia recurvata* in Argentina which do have more or less entire leaf pseudomargins (Fig. 29, leaves *f, g, j, o, p, q*). This form, designated "triceps" here, has bracts which are usually curved outward as they are in the "beckii" form, but has blue rather than yellow flowers and does not have the stiff white spines of the "beckii" form. There is a tendency for plants in these populations to have 2 or 3 heads per flowering stem.

Previous workers, also conscious of the complex situation, have merged the forms to various, but not necessarily identical, degrees. Hooker saw the plants in the field and observed in the Flora Antarctica (p. 322, 1847) that *Perezia beckii* was extremely variable in the amount of spines on the leaf margins, and some plants lacked them altogether. The species described as *P. patagonica, P. patagonica* var. *intermedia* and *P. reflexa* all seem to me to be merely smooth leaved plants of the "beckii" form.

Reiche, in the Flora of Chile (1905) observed that *Perezia linearis, P. pectinata, P. triceps, P. doniana,* and *P. reflexa* could probably be grouped into two or three species. He felt that one good species would be *P. linearis* (which is maintained in this work as a distinct species) with flat, non-recurved leaves. Whether or not the plants with recurved leaves constituted one species, he felt, depended on whether future investigations showed that plants with monocephalous and polycephalous flowering stems occurred in the same population. Evidence now demonstrates that both types of plants can come from the same population.

As is clearly shown in Fig. 28, there is no tendency for the three principal phenotypes to cluster into groups when "important" characters are plotted. Although there is variation, the plants show complete intergradation in the size of the bracts and leaves. Thus the only character which could separate the presumed species would be the leaf margin (and the bract margins, but these are correlated with the leaf margins). However, even this character is completely unreliable.

In areas where distinct phenotypes come into contact (Fig. 27–4 at such points as Lago Cardiel, Pilcaniyeu, Río Gallegos, Lago Argentino—all in Argentina), intermediate forms are abundant and there is a complete sequence of leaf types (Fig. 29). Yet, two phenomena present in *Perezia recurvata* still need ex-

planation. First, why do the major phenotypes occupy more or less defined geographical ranges (Fig. 27–4) and, secondly, why are there plants of extremely variable morphology (i.e., in leaf margin) even well within the range of a given phenotype?

The complex type of variation seen in *Perezia recurvata* could have resulted from two causes—or a combination of the two. This species could be composed of populations which had been isolated at some period and underwent a small amount of morphological divergence but little or no reproductive change. After the barriers separating the populations were removed, the forms expanded their ranges and came into secondary contact. In the areas of secondary overlap, a stepped cline in morphology would be visible. This type of narrow band of intermediate forms between recognizable geographical races (see distribution map, Fig. 27–4) in such areas as Pilcaniyeu, Lago Cardiel, and Río Gallegos approximates the theoretical case of secondary overlap between partially isolated forms of the same taxon.

A second possibility is that the phenotypes now present in the species are simply the result of selection following a micro-ecological gradient. There is some evidence that this is the case in the populations described by Hooker where plants seem to have dense spines randomly along the leaf edges, or be entirely smooth margined. Controlled plantings of a smooth leaf form from Bariloche, Argentina (the "triceps" form) were made at Cambridge, Massachusetts. Under the greenhouse conditions, the plants became elongate and had longer leaves than the plants from which the seeds had been taken. Also, the leaf edges of the Cambridge plants bore small spines on the leaf margins. The external morphology is, of course genetically determined, but in situations where the environment is variable, the plants seem to have the potential for some morphological modification. Such a situation is common and has been well understood since the work of Clausen, Keck and Hiesey (1940, 1945, 1948).

Both of the factors mentioned seem to underlie the pattern now seen in *Perezia recurvata*. There is definitely some modification due to environmental conditions, but one phenotype can never completely change into another. However, over a period of generations, with a necessary amount of selection pressure, any of the forms could be produced. In the case of *P. recurvata*, I feel that selection acted on three isolated groups of populations. One

"pro-recurvata" series of populations was isolated in southeastern South America, near or on Tierra del Fuego and the Falkland Islands. Another "pro-triceps" group of populations was isolated in northwestern Patagonia in the region near Nahuel Huapí. The third cluster of "pro-beckii" populations would have been isolated in northeastern Patagonia somewhere south of Bahia Blanca. The factors which caused the isolation of these populations would have been the series of Pleistocene glaciofluvial lakes and rivers which abounded in Patagonia during the Ice Ages. After the Pleistocene glacial retreats and the post-Pleistocene drying, the three groups of populations reexpanded their ranges and produced the pattern of secondary contact now visible.

The question now arises as to whether it is necessary to give the forms recognition as subspecies or varieties. A subspecies is usually an allopatric population or series of populations distinct enough to be recognized as belonging to a defined taxon (Mayr, 1963, p. 672). In the case of *Perezia recurvata,* all the forms come in contact and form intermediates which would be impossible to place in one or another of the "subspecies." However, it must be admitted that there is only a very narrow zone of intermediacy between two forms apparent from the specimens I have seen. Nevertheless, I have acted to keep the complex as a single species without subspecific parts, fully recognizing it to be highly polymorphic and variable.

EXCLUDED SPECIES

1. *Perezia lanigera* Hooker & Arnott, Comp. Bot. Mag. **2**:42. 1836. Type: ARGENTINA. Port Desire, *Darwin 314* (K).

Perezia sessiliflora Spegazzini, Rev. Fac. Agron. Vet. **3**:542. 1897. Type: ARGENTINA. Rio Santa Cruz, 1897, *Spegazzini* (type not seen).

This species is excluded from the genus *Perezia* because it has dense woolly trichomes in the leaf axils, only two rows of involucral bracts, and achenes with a type of pubescence not found in any South American species of *Perezia.* Similar trichomes were described for the genus *Trixis* by Small (1919) and for *Senecio* by Hess (1938). The interior substance of this type of trichome is extruded when the achene becomes wet. Obviously, however, the species belongs in neither *Trixis* nor *Senecio.* Its exact generic placement must await further work on the other genera of the *Nassauviinae.*

2. *Perezia glandulosa* Meyen, Reise um die Erde 470. 1834. Meyen's description is totally inadequate and I can find no specimen annotated by him. Although Walpers later placed this species in synonymy with *P. ciliaris,* it is not clear from the description that it belcngs with this taxon. Since Meyen's name is older than *P. ciliaris* and would necessitate a name change if the two were merged, it seems best to avoid further complication by excluding Meyen's name.

3. *Perezia spathulata* Philippi, Anal. Univ. Chile **87**:300. 1894. non *Clarionea spathulata* Lag. ex D. Don (=*Perezia viscosa* Lessing). Type: CHILE. Curíco: Cordillera de Curíco, Restate, 1889, *no collector* (SGO).

This taxon is probably synonymous with *Leucheria foliosa* Philippi.

4. *Perezia pampeana* Spegazzini, Fl. Tandil 33. 1901. (type not seen). According to Cabrera (Compuestas Bonaerensis, Rev. Mus. La Plata II. 4:379. 1941) this species is a synonym of *Trixis stricta* (Sprengel) Lessing.

LITERATURE CITED

AHLFELD, F. AND L. BRANIŠA. 1960. Geología de Bolivia. Instituto Boliviano de Petroleo, La Paz, Bolivia. 245 pp.

ALSTON, R. E. 1967. Biochemical Systematics. Evol. Biol. **1**:197–305.

ALSTON, R. AND B. L. TURNER. 1963a. Natural Hybridization among Four Species of *Baptisia* (Leguminosae). Am. Jour. Bot. **50**:159–173.

————————. 1963b. Biochemical Systematics. Prentice-Hall. Englewood, New Jersey. 404 pp.

AMEN, R. D. 1966. The Extent and Role of Seed Dormancy in Alpine Plants. Quart. Rev. Biol. **41**:271–281.

ARANO, H. 1957. The Karyotype Analysis and its Karyotaxonomic Considerations in the Tribe Mutisieae. Jap. Jour. Genet. **32**:293–299.

————————. 1963. Cytological Studies in Subfamily Carduoideae (Compositae) of Japan IX. The Karyotype Analysis and Phylogenic Considerations on *Pertya* and *Ainsliaea*. Bot. Mag. Tokyo **76**:32–39.

AUER, V. 1956. The Pleistocene of Fuego-Patagonia. Part I: The Ice and Interglacial Ages. Ann. Acad. Sci. Fenn. Ser. A. III. Geol. Geogr. **45**:1–226.

BACIGALUPI, R. 1931. A Monograph of the Genus *Perezia*, Section *Acourtia*, with a Provisional Key to the Section *Euperezia*. Contr. Gray Herb. **97**:1–81.

BAKER, J. G. 1884. Compositae. Mutisiaceae. *In* Martius, C. F., Fl. Bras. **4**(3):339–398.

BALDWIN, J. T. AND B. M. SPEESE. 1947. *Chaptalia nutans* and *C. integrifolia:* Their Chromosomes. Bull. Torrey Club **74**:283–286.

BENTHAM, G. 1873. Notes on the Classification, History and Geographical Distribution of Compositae. Jour. Linn. Soc. Bot. **13**:335–577.

BENTHAM, G. AND J. D. HOOKER. 1873. Compositae. Genera Plant. **2**:163–533.

BERRY, E. W. 1917. Fossil Plants from Bolivia and their Bearing upon the Uplift of the Andes. Proc. U. S. Natl. Mus. **54**:103–164.

————————. 1919. Miocene Fossil Plants from Northern Perú. Proc. U. S. Natl. Mus. **55**:279–294.

————————. 1922a. Contributions to the Paleobotany of Perú, Bolivia, and Chile. The Flora of the Concepción-Arauco Coal Measures of Chile. Johns Hopkins Univ. Stud. Geol. **4**:73–143.

————————. 1922b. Contributions to the Paleobotany of Perú, Bolivia, and Chile. Pliocene Fossil Plants from Eastern Bolivia. Johns Hopkins Univ. Stud. Geol. **4**:145–203.

————————. 1925. A Miocene flora from Patagonia. Johns Hopkins Univ. Stud. Geol. **6**:183–251.

————————. 1937a. Succession of Fossil Floras in Patagonia. Proc. Natl. Acad. U. S. **23**:537–542.

————————. 1937b. An upper Cretaceous flora from Patagonia. Johns Hopkins Univ. Stud. Geol. **12**:1–31.

————————. 1938. Tertiary Flora from the Río Pichulefu, Argentina. Geol. Soc. Am. Special Paper **12**:1–149.

Bliss, L. C. 1956. A Comparison of Plant Development in Microenvironments of Arctic and Alpine Tundras. Ecol. Monogr. **26**:303–337.

Boelcke, O. 1957. Communidades Herbáceas del Norte Patagonia y sus Relaciones con la Ganaderia. Revista Invest. Agr. Buenos Aires **11**:5–98.

Brehm, B. G. 1966. Taxonomic Implications of Variation in Chromatographic Pattern Components. Brittonia **18**:194–202.

Brüggen, J. 1950. Fundamentos de la Geología de Chile. Inst. Geogr. Militar, Santiago. 374 pp.

Cabrera, A. L. 1939. Las Compuestas del Parque Nacional del Nahuel Huapí. Revista Mus. La Plata Bot. **2**:227–396.

————————. 1965. Revisión del Género *Mutisia* (Compositae). Opera Lilloana **13**:1–227.

Caldenius, C. C. 1932. Las Glaciaciones Cuaternarias en la Patagonia y Tierra del Fuego. Geogr. Annaler **14**:1–164.

Candolle, A. P. de. 1838. Nassauviaceae. *In* Prodr. Sys. Nat. **7**(1):48–74.

Candolle, M. de. 1812. Observations sur les Plantes Composées, ou Syngenèses. Troisième Mémoire. Sur les Composées à Corolles Labiées, ou Labiatiflores. Ann. Mus. Hist. Nat. Paris **19**:59–72.

Carlquist, S. 1957. Anatomy of Guayana Mutisieae. Mem. N. Y. Bot. Gard. **9**:441–476.

Cassini, H. 1817. Dict. Sci. Nat. Paris 8:395.

————————. 1821. Dict. Sci. Nat. Paris **20**:378.

————————. 1826. Les Nassauviniées. *In* Opuscules Phytologiques **2**:151–201.

Clausen, J., D. D. Keck and W. M. Hiesey. 1940. Experimental Studies on The Nature of Species I. Carnegie Inst. Publ. **520**:1–452.

————————. 1945. Experimental Studies on the Nature of Species II. Carnegie Inst. Publ. **564**:1–174.

————————. 1948. Experimental Studies on the Nature of Species III. Carnegie Inst. Publ. **581**:1–129.

Coleman, J. R. 1968. Chromosome Numbers in some Brazilian Compositae. Rhodora **70**:228–240.

Covas, G. and B. Schnack. 1946. Número de Chromosomas en Antófitas de la Región de Cuyo (Republica Argentina). Revista Arg. Agron. **13**:153–166.

————————. 1947. Estudios Cariológicos en Antófitas. II Parte. Revista Arg. Agron. **14**:224–231.

Darlington, C. D. and A. P. Wylie. 1955. Chromosome Atlas of Flowering Plants. Allen and Unwin. London. 519 pp.

Dejong, D. C. D. and E. K. Longpre. 1963. Chromosome Studies in Mexican Compositae. Rhodora **65**:225–240.

Diers, L. 1961. Der Anteil an Polyploiden in den Vegetationsgürteln der Westkordillere Perus. Zeits. Bot.: 437–488.

Drury, D. G. and L. Watson. 1965. Anatomy and the Taxonomic Significance of Gross Vegetative Morphology in *Senecio*. New Phytol. **64**:307–314.

————————. 1966. Taxonomic Implications of a Comparative Anatomical Study of Inuloideae-Compositae. A. Jour. Bot. **53**:828–833.

Eades, D. C. 1965. The Inappropriateness of the Correlation Coefficient as a Measure of Taxonomic Resemblance. Syst. Zool. **14**:98–100.

Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy. Angiosperms

(An Introduction to Palynology I). The Chronica Botanica Co. Waltham, Mass. 539 pp.
————————. 1960. The Acetolysis Method. Sv. Bot. Tidskr. **54**:561.
GERTH, H. VON. 1941. Die Tertiärfloren des südlichen Südamerika und die angebliche Verlagerung des Südpols während dieser Periode. Geol. Rundschau **32**:321–336.
GODLEY, E. J. 1960. The Botany of Southern Chile in Relation to New Zealand and the Subantarctic. Proc. Roy. Soc. London B **152**:457–475.
GRAY, A. 1883. Contributions to North American Botany. Proc. Am. Acad. Sci. **19**:1–96.
————————. 1884. Synoptical Flora of North America. Vol. 1. Part 2. Ivison, Blakeman, Taylor and Co. New York.
GROEBER, P. 1936. Oscillaciones de Clima en la Argentina desde el Plioceno. Holmbergia **1**(2):71–84.
HADLEY, E. B. AND L. C. BLISS. 1964. Energy Relationships of Alpine Plants on Mount Washington, New Hampshire. Ecol. Monogr. **34**:331–357.
HEDBERG, O. 1964. Features of Afroalpine Plant Ecology. Acta Phytogeogr. Suec. **49**:1–144.
HEISER, C. 1963. Numeración Chromosómica de Plantas Ecuatorianas. Ciencia y Naturaleza **6**:2–6.
HESS, R. 1938. Vergleichende Untersuchungen über die Zwillingshaare der Compositen. Bot. Jahrb. **68**:435–496.
HOFFMANN, O. 1893. Mutisieae. Compositae. *In* Engler and Prantl. Die natürlichen Pflanzenfamilen 4(5):333–350.
HOOKER, J. D. 1847. Flora Antarctica. Vol. 2. Reeve Brothers. London.
HOSSEUS, C. C. 1915. La Vegetación del Lago Nahuel Huapí y sus Montañas. Trab. Inst. Bot. y Farm. **33**:1–102.
HULTÉN, E. 1937. Outline of the History of Arctic and Boreal Biota During the Quaternary Period. Bokförlags Aktiebolaget. Stockholm. 168 pp.
————————. 1955. The Isolation of the Scandinavian Flora. Acta Soc. Fauna Fl. Fenn. **72**(8):1–22.
HUMBOLDT, A. AND A. BONPLAND. 1809. Plantae Aequinoctiales. Tomus 2. Apud F. Schoell. Paris.
KEMP, W. B. 1937. Natural selection within plant species as exemplified in a permanent pasture. Jour. Heredity **28**:328–333.
LAGASCA, M. 1811. Disertación sobre un Orden Nuevo de Plantas de la Clase de las Compuestas. Amen. Nat. de las Españas **1**:26–44.
LANJOUW, J. AND F. A. STAFLEU. 1964. Index Herbariorum, Regnum Vegetabile 31. International Bureau for Plant Taxonomy and Nomenclature, Utrecht, Netherlands. 251 pp.
LAUER, W. 1952. Humide und aride Jahrszeiten in Afrika und Südamerika und ihre Beziehung zu den Vegetationsgürteln. Bonner Geogr. Abh. 9.
LESSING, C. F. 1832. Synopisis Generum Compositarum. Berolini. Paris, France. 473 pp.
MAYR, E. 1963. Animal Species and Evolution. Harvard University Press. Cambridge, Mass. 797 pp.
MCCLURE, J. W. AND R. ALSTON. 1966. Chemotaxonomy of the Lemnaceae. Am. Jour. Bot. **53**:849–859.
METCALFE, C. R. AND L. CHALK. 1965. Anatomy of the Dicotyledons. Vol. 2: 782–804. Oxford University Press. London.
MINKOFF, E. C. 1965. The Effects on Classification of Slight Alterations in Numerical Technique. Syst. Zool. **14**:196–213.
MOONEY, H. A. AND W. D. BILLINGS. 1965. Effects of Altitude on Carbohydrate Content of Montane Plants. Ecology **46**:750–751.

Nees, C. G. von Esenbeck and K. F. P. von Martius. 1824. Beiträge zur Flora Brasiliensis. Nova Acta Acad. Leop.-Carol. **12**:5 t. 1.
Polanski, J. 1965. The Maximum Glaciation in the Argentine Cordillera. Geol. Soc. Am. Special Paper **84**:453–472.
Pyykkö, M. 1966. The Leaf Anatomy of East Patagonian Xeromorphic Plants. Ann. Bot. Fenn. **3**:453–622.
Rao, C. R. 1952. Advanced Statistical Methods in Biometric Research. John Wiley. New York.
Reiche, K. 1905. Flora de Chile **4**:435–455. Cervantes. Santiago, Chile.
Rogers, D. J., H. S. Fleming and G. Estabrook. 1967. Use of Computers in Studies of Taxonomy and Evolution. Evol. Biol. **1**:169–196.
Simpson, G. G., A. Roe and R. C. Lewontin. 1960. Quantitative Zoology, Revised edition. Harcourt, Brace and Company. New York. 440 pp.
Skottsberg, C. 1916. Die Vegetationsverhältnisse längs der Cordillera de los Andes S. von 41° S. Br. Sv. Vet-akad. Handl. **56**(5):1–366.
Small, J. 1919. The Origin and Development of the Compositae. New Phytol. Reprint **11**:1–334. (A reprint of a series of articles which appeared in the New Phytol. during 1917–1919.)
Sokal, R. R. and C. D. Michener. 1958. A Statistical Method for Evaluating Systematic Relationships. Univ. Kansas Sci. Bull. **38**:1409–1438.
Sokal, R. R. and P. H. A. Sneath. 1963. Principles of Numerical Taxonomy. Freeman and Co. London. 359 pp.
Solbrig, O. 1960. Leaf Venation and Pubescence in the Genus *Raoulia* (Compositae). Jour. Arnold Arb. **41**:259–269.
Spegazzini, C. 1897. Plantae Patagoniae. Revista Fac. Agron. Vet. **3**(30–31):485–598.
————————. 1901. Contribución al Estudio de la Flora del Tandil. Sessé. Larrañaga y Renovales, La Plata, Argentina.
Stebbins, G. L. 1950. Variation and Evolution in Plants. Columbia University Press. New York. 643 pp.
Thomasson, K. 1959. Nahuel Huapí. Acta Phytogeogr. Suec. **42**:1–83.
Tovar, O. 1955. Revisión de las Especies Peruanas del Género *Perezia*. Publ. Mus. Hist. Nat. Lima Bot. **8**:1–35.
Troll, C. 1959. Die tropischen Gebirge. Ihre dreidimensionale klimatische und pflanzengeographische Zonierung. Bonner geogr. Abh. **25**:1–93.
Vahl, M. 1790. Om *Perdicium* og dens Argen om en ny Slaegt *Rohria,* henhørende til Compositae. Skr. Naturh.-Selsk. Kjøbenh. **1**(2):1–17.
Vuilleumier, F. 1967. Phyletic Evolution in Modern Birds of the Patagonian Forests. Nature **215**:247–248.
————————. 1968. Origin of Frogs of Patagonian Forests. Nature **219**:87–89.
Weddell, H. A. 1855. Chloris Andina **1**:36–45. Chez P. Bertrand. Paris, France.
Weberbauer, A. 1945. El Mundo Vegetal de los Andes Peruanos. Editorial Lumen, S.A., Lima, Peru. 776 pp.
Wilhelmy, H. 1957. Eiszeit und Eiszeitklima in den feuchttropischen Anden. Petermanns Geogr. Mitt. Ergänzungscheft **262**:281–309.
Wodehouse, R. P. 1928a. Pollen Grains in the Identification and Classification of Plants. I. The Ambrosiaceae. Bull. Torrey Club **55**:181–198.
————————. 1928b. Pollen Grains in the Identification and Classification of Plants. II. *Barnadesia*. Bull. Torrey Club **55**:449–462.
————————. 1929a. Pollen Grains in the Identification and Classification of Plants. III. The Nassauvinae. Bull. Torrey Club **56**:123–138.
————————. 1929b. Pollen Grains in the Identification and Classification of Plants. IV. The Mutisieae. Am. Jour. Bot. **16**:297–313.

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THE CLASSIFICATION OF THE CYATHEACEAE

ROLLA TRYON

The *Cyatheaceae* is a moderate-sized family of about 650 species nearly equally divided between the neotropics and the paleotropics. The greatest number of species is found in the relatively cool and more or less constantly moist zones of tropical mountains. This feature may be seen in Fig. 1, where, within the distribution of the family in America, the areas of high concentrations of species correlate with the principal areas of cloud forest and montane forest.

I am not including the members of the *Dicksoniaceae* within the *Cyatheaceae* as Holttum and Sen (1961) have recently done. While appreciating the characters that they have brought to the classification, I believe that more information is needed before the evolutionary lines in the Dicksonioid-Cyatheoid alliance can clearly be traced, and the family (or families) recognized with assurance. There is, for example, some evidence which suggests that *Lophosoria* and *Metaxya* may be closer to the *Dicksoniaceae* than to the scaly *Cyatheaceae*. It is the classification of the scaly members of the *Cyatheaceae* which is my present concern and I have left in abeyance the problems raised by the Dicksonioid genera. I am tentatively following Christensen (1938) in recognizing the *Cyatheaceae* as including those genera that have a dorsal sorus.

A few years ago I began a systematic study of the American *Cyatheaceae* and this paper is the first report of the work. I recognize eight genera in the family, one of them new and the others, except for the monotypic *Lophosoria* and *Metaxya,* variously enlarged or remodeled and mostly redefined on the basis of new characters. My initial studies were directed toward the evolutionary developments in the family and the recognition of evolutionary groups which could form the basis of a generic classification. This survey indicated that there was greater morphological diversity among the American members of the family than among those of the Old World. For this reason, it was not possible to integrate the American species into the classification of Holttum (1963, 1964, 1965) which was developed principally on the basis of paleotropical species.

The six main groups of the squamate species have been recog-

nized as genera on the basis of the evidence that each is a major evolutionary line. Some of these genera are more distinctive and better defined than others, and some have more evolutionary innovations than others. There is no certain guide for the recognition of a group of species as a genus and I have chosen to admit to generic status only groups with substantial evolutionary qualifications, either in distinctiveness or in extensive speciation. The more distinctive genera need not have a large number of species while those that have many species may be less distinctive.

FIG. 1. Map of the distribution of Cyatheaceae in America and (in black) the areas of high concentrations of species: Hispaniola and Jamaica, 40 species; Costa Rica, 45 species; Andes, 125 species; southeastern Brazil, 40 species.

The present classification is based on a study of about 275 American species and about 230 species of the Old World. Approximately 75 per cent of the known species, from all parts of the range of the family and including species of all proposed groups, has been examined. Confidence in the classification has developed since its inception, as it has been brought into ever sharper focus by the incorporation of data from additional species and additional characters.

An unsatisfactory classification has persisted in the *Cyatheaceae* for a longer time than in any other of the large groups of ferns. There is no purpose in a historical discussion of the futile efforts to classify the family. It is sufficient to point out that prior to the work of DeWolf (1953) and of Holttum (1957, 1963), no progress was made toward the development of a realistic classification based on evolutionary developments in the family. It is true that some small segregate genera were proposed earlier that now can be recognized as natural groups, but these proposals (and others that lacked merit) did not improve the classification of the large and heterogeneous assemblage that remained.

The vital clue to the classification of the family was discovered by DeWolf (1953) in his studies of the petiole scales of paleotropical species, where he brought out the difference between "setiferous" (conform) and "flabelloid" (marginate) scale types. These studies were suggested by Holttum, who later (1957, 1963) successfully used the petiole scales over a very wide range of species in developing the classification of his inclusive genus *Cyathea.* In his classification the subgenera *Cyathea* and *Sphaeropteris* were based on the "flabelloid" and the "setiferous" scales respectively. Holttum's several papers (see Literature Cited) have provided the first broad foundation for the modern classification of the family.

My own intensive study of the American species has resulted in some taxonomic and evolutionary conclusions different from those of Holttum; this is probably inevitable as progress is made in the study of a large and complex group. Further attention to the morphology of the petiole scales has added to the diversity of scale types in the family and has provided the basis for the recognition of three principal evolutionary lines. The scale morphology, even when not wholly distinctive (for example, in

Nephelea and *Cnemidaria*) has been an important aid in the recognition of tentative evolutionary groups which have then been confirmed by further study of other characters.

CHARACTERS

A wide range of characters has been studied during the course of this investigation, most of which have not been usable at the generic level. Some are significant for species or species-groups; others, especially those of the stem, have not been represented in a sufficient number of species. Characters of the stem deserve careful attention but many more collections must be made before their significance can be assessed. Among the characters employed in this paper, some require explanation and these are discussed in the following paragraphs.

The petiole is sometimes smooth but more commonly, especially toward its base and on its abaxial side, it is variously roughened or spiny. A petiole that is pubescent sometimes becomes *scabrous* as the trichomes break off and leave a persistent base. In most species the petiole scales are borne on slight to very prominent projections of the petiole and these persist when the scale falls. When these projections are very low, the petiole is *muricate;* when they are larger but rounded and about as tall as broad, the petiole is *tuberculate;* when they are taller and tapering at the apex, they are called *spines,* and the petiole is *aculeate.*

In most of the aculeate species, the spines have evidently evolved by a development of the tissues of the petiole beneath the scale. I call these *corticinate* spines (cortex + natus: born of the cortex of the petiole). These can readily be identified in suitable material because a complete scale is perched on top of the spine (Fig. 22). The scale is sometimes not clearly differentiated from the apex of the spine, suggesting that the apex may be partly formed from the base of the scale. There is a complete transition from species with a smooth petiole to those with large spines of the corticinate type.

In other species the spines (Fig. 31) have evidently evolved by development of the body of the scale and the tissues of the petiole have not been involved in their formation. These are called *squaminate* spines (squama + natus: born of a scale). This kind of spine can be readily identified on suitable material because

some of the smaller spines will bear, on each side, the differentiated margin of the normal scale (Fig. 34). Rarely, an unmodified portion of the scale extends beyond the apex of the spine. There is a transition in *Alsophila* from species with normally developed scales to those with spinelike scales and to one species with squaminate spines. The evidence for the origin of this type of spine from a petiole scale is discussed more fully under the genera *Nephelea* and *Alsophila*.

It is sometimes necessary to refer to different parts of the petiole scales and to different kinds of scales. The *body* of the scale is considered to be the whole scale except for such processes (cilia, teeth, setae) as may be borne on the edge or at the apex. The *edge* of the scale is considered to consist of the single row of ultimate cells, or when cilia, teeth or setae are present, sometimes an additional row of cells that may be related to those processes.

The petiole scales of *Sphaeropteris* have all the cells of the body similar in shape and orientation (elongate with their long axis parallel to that of the scale) and usually in size and color (for example, Figs. 14–17). This kind of scale is called *structurally conform* or simply *conform*. In the other genera, the central cells of the petiole scales are also elongate and parallel to the long axis of the scale, but toward each edge the cells are different in size and orientation, and (usually) in shape and color (for example, Fig. 27). The central area of elongate cells then is called the *central portion* and the differentiated area (on each side) the *margin*. This kind of scale is called *structurally marginate*, or simply *marginate*. The margin may be broad or narrow and it may be well or poorly defined depending on the abruptness of the transition between the elongate cells of the central portion and the differentiated cells near the edge.

In many species there is a *minute indument* on the surface of the petiole that consists of very small scales or trichomes. These are composed of only a few cells. The small scales of this indument are called *squamulae* and the small trichomes *trichomidia*.

The indusium may completely surround the base of the receptacle, or not, and it may be variously developed. Very small indusia that are attached to one part of the base of the receptacle are called *scale-like*. Moderately to well developed indusia that partially surround the base of the receptacle are called *hemitelioid*.

Well developed indusia that completely surround the base of the receptacle are called *cyatheoid* if they are open at their apex, and *sphaeropteroid* if they are closed at their apex.

EVOLUTION

Among the squamate genera the characters of the petiole scales define three groups which I believe reflect the basic evolutionary lines: the genus *Sphaeropteris* with structurally conform petiole scales (Figs. 14–21), the genera *Alsophila* and *Nephelea* with structurally marginate petiole scales having dark apical setae (Figs. 23–30, 35–36), and the genera *Trichipteris, Cyathea* and *Cnemidaria* also with structurally marginate petiole scales but without apical setae (Figs. 39–41, 44–47). These three groups are evident in the phyletic chart (Fig. 2).

Within *Sphaeropteris, Alsophila* and *Nephelea,* further evolutionary developments occur that involve a thickening of the petiole scales. In a number of species of *Sphaeropteris* of Malaysia and Polynesia, the scales are basally thickened and rather fleshy. These species were recognized as *Cyathea* subsection *Sacropholis* by Holttum (1963). A similar development is also evident in some species of *Alsophila* of the West Indies, especially in *Alsophila Urbanii* which has small scales definitely thickened and somewhat fleshy. In other species of *Sphaeropteris* and *Alsophila* and in *Nephelea* the thickened petiole scales are hard and rigid. In *Sphaeropteris procera* of New Guinea some of the scales are quite modified and spine-like; and in *Alsophila auriculata* of Madagascar and in *Nephelea* the thickened and rigid scales form a transition from the normal scales on the petiole to the petiolar spines.

In a general way, it is possible to postulate an adaptive basis for the origin of scales and their structural differentiation. The arborescent habit elevates the apex of the stem with its crown of large leaves far above the root system. This must create problems in water relations that require some compensating adaptations. Any evolutionary development that would aid the roots and tall stem in providing water to the apex would contribute toward the solution of this problem. A dense investment of scaly indument could provide a better means for the absorption of water in the form of fog or rain than an investment of trichomes. The effective-

ness of the scales in water absorption could be improved by different orientations of the scales (Figs. 3, 4) and differences in their cellular construction. This concept provides an evolutionary rationale for the development and differentiation of the petiole scales. It also provides a basis for the conclusion that the developments in the petiole scales have been basic to the establishment of the major evolutionary lines in the squamate group.

I adopt the view that the genera with scales have evolved from ancestors having an indument wholly of trichomes. There are a few species among American *Sphaeropteris* that have petiole scales quite undifferentiated in cellular structure and two of these also have the scales intergrading to trichomes. In these species, *Sphaeropteris macarenensis* and *S. mollicula,* there are long trichomes on the petiole as well as long narrow scales that vary from two to many cells broad (Figs. 5–9). The cells of the scales are similar in size and proportion to those of the trichomes (compare Fig. 5 with 6 and 7). The base of some of the narrow scales is uniseriate (stipitate) (Fig. 6). The structure of these suggests that the first stage in the development of a scale has been a pluriseriate development above the base of a trichome. I consider that *Sphaeropteris macarenensis* and *S. mollicula* are primitive among the scaly species in respect to both their undifferentiated petiole scales and their petiole indument that shows the transition from trichomes to scales.

The origin of the indusium in the *Cyatheaceae,* and its evolutionary significance, has been subject to considerable disagreement. Bower (1926, Chapter 33) considered the exindusiate condition of the sorus to be primitive and the indusium to be a new structure which evolved later. Holttum and Sen (1961) and Sen (1964) interpret the indusium as homologous with that of *Dicksonia,* marginal in origin and the hemitelioid indusium as primitive. I believe that evidence from three sources supports Bower's interpretation that the indusium has originated from a laminar scale attached to the base of the receptacle. In the exindusiate species *Trichipteris armata,* there is usually a small scale closely associated with the receptacle but not attached to it (Riba, 1969). This scale is borne, slightly toward the midvein, on the vein that bears the receptacle. There is a small group of species in Malaysia and Polynesia (*Cyathea* subsection *Fourniera,* Holttum 1963, 1964) that has thin scales investing the sorus,

arising from the base of the receptacle. Finally, there are some species, for example *Cyathea Tuerckheimii,* in which a sphaeropteroid indusium bears an apical squamoid development (Fig. 10). This evidence strongly suggests an intimate relation between a laminar scale and an indusium, which I interpret to mean that the indusium is of squamate origin and that the indusiate sorus has been derived from the exindusiate sorus. The exindusiate condition of *Sphaeropteris macarenensis* and *S. mollicula* is consistent with the conclusion, drawn from their petiole indument, that they are species with primitive characters.

Sphaeropteris macarenensis and *S. mollicula* are different in some characters of the sorus from other scaly species. These characters are their slightly to moderately elevated receptacle, relatively few sporangia in a sorus and nearly globose sporangium capsule. In these soral characters the two species are rather similar to *Lophosoria* as indicated in Table 1. The comparisons presented there include characters of the petiole indument, the sorus and indusium and also the contrasting characters of a scaly indusiate species. It is reasonable to consider the wholly pubescent *Lophosoria* as representing a lower evolutionary level than the scaly genera of the family and the similarities in soral characters between it and *Sphaeropteris macarenensis* and *S. mollicula* suggest that those species are also at a rather low evolutionary level.

These considerations, summarized in Table 1, are all consistent with the conclusion that *Sphaeropteris macarenensis* and *S. mollicula* are species with primitive characters and are the most primitive of the living scaly species. Thus *Sphaeropteris* is taken as the most primitive of the scaly genera.

The phyletic relations of the genera are presented in Fig. 2. *Lophosoria* and *Metaxya* are placed apart in order to avoid the implication that either is directly ancestral to the group of scaly genera. *Sphaeropteris* is considered to have been derived from an ancestral line on an evolutionary level similar to that of *Lophosoria* but not necessarily one that would be congeneric with it. The first development of an indusium occurred in some species of *Sphaeropteris* and in one line setae were developed at the apex (and usually along the edge) of the petiole scales. A major evolutionary line has developed from each of the petiole scale types in *Sphaeropteris*. The setate type has given rise to *Alsophila* by the differentiation of the margin on the petiole scale and then to

TABLE 1

CHARACTERS OF FOUR SPECIES OF CYATHEACEAE

	Lophosoria quadripinnata	*Sphaeropteris macarenensis*	*Sphaeropteris mollicula*	*Cyathea arborea*
Petiole indument	trichomes only	trichomes intergrading to undifferentiated scales		Broad, differentiated scales
Receptacle	low	slightly elevated	moderately elevated	strongly elevated
Number of sporangia in a sorus	ca. 6–12	ca. 8–12	ca. 9–15	ca. 25–50
Sporangium capsule	asymmetrically globose	asymmetrically globose	asymmetrically globose	asymmetrically elongate-compressed
Indusium	none	none	none	cyatheoid

Nephelea by the development of squaminate spines on the petiole. Some species of *Alsophila* are exindusiate, indicating that the indusium evidently originated at least once in this line. An exindusiate group in *Sphaeropteris* with petiole scales lacking dark setae has given rise to the genera *Trichipteris, Cyathea* and *Cnemidaria,* again by a differentiation of the margin on the scale. The exindusiate *Trichipteris* gave rise to *Cyathea* by an independent development of the indusium. *Cnemidaria* has evolved in lamina reduction and vein modification especially; it was probably derived from species of *Cyathea* in which the indusium was only partially developed. This phyletic scheme provides a framework within which other evolutionary developments can be placed and provides an indication of the general evolutionary level of the genera.

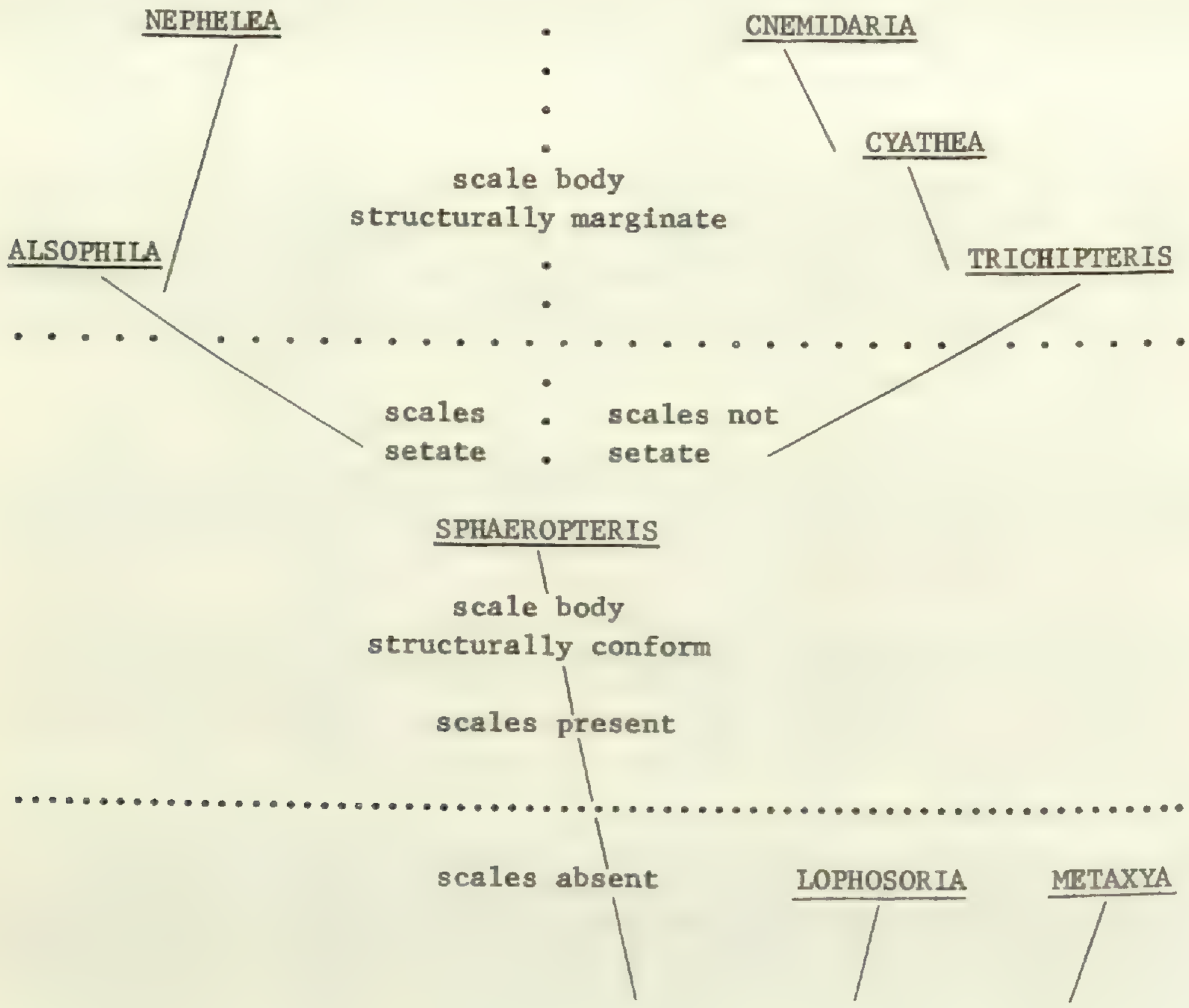
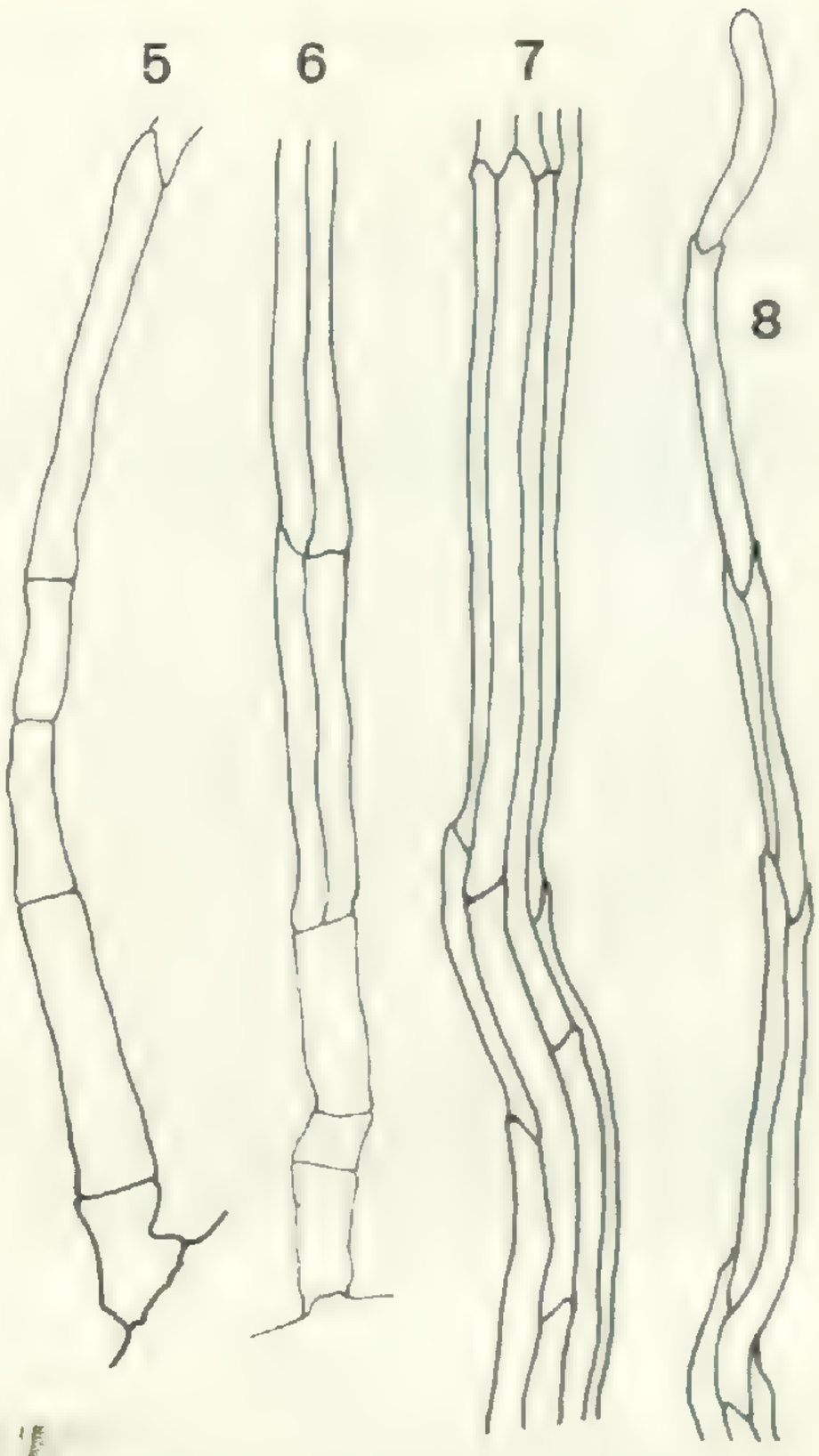
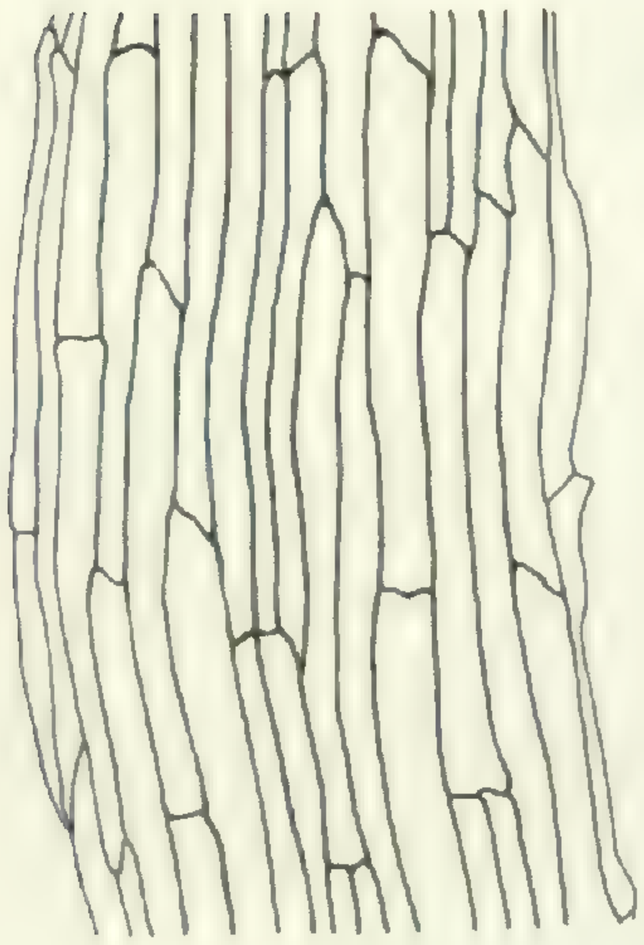
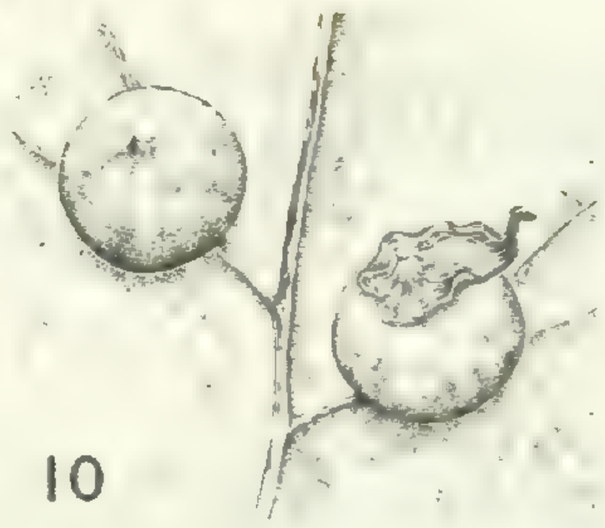
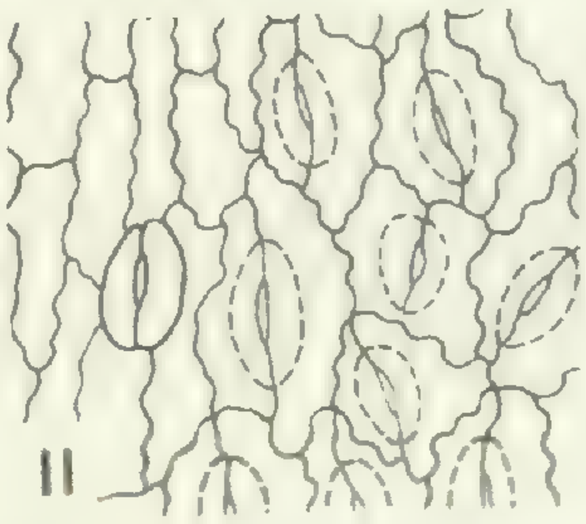


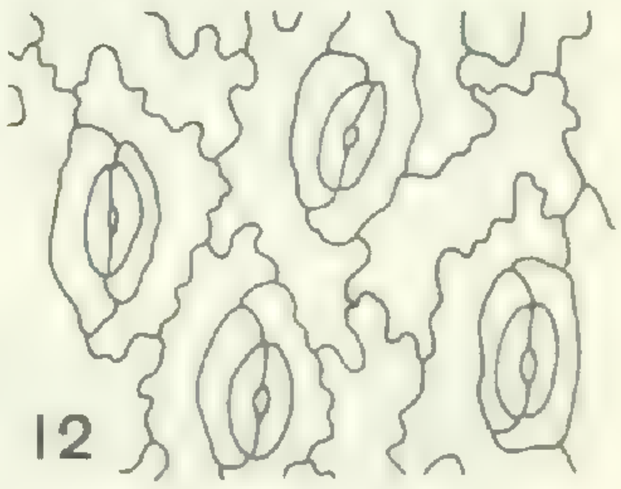
FIG. 2. Phyletic chart of Cyatheaceae.











FIGS. 3–13. CYATHEACEAE. FIGS. 3–4. Longitudinal sections of the stem apex, the older croziers removed, the scales are very tightly packed and the lines indicate only the general orientation and size, not the individual scales: 3, Small, patent scales of *Nephelea aureonitens, Gastony 763,* × 1/2, GH, 4, Larger, imbricate scales of *Cyathea conspersa, Tryon & Tryon 7025,* × 1/2, GH. FIGS. 5–9. Petiole indument of *Sphaeropteris macarenensis, Schultes & Cabrera 13368,* all × 60, A:5, Basal portion of trichome. 6, Basal portion of scale two cells wide. 7, Central portion of narrow scale. 8, Apex of scale in Fig. 7. 9, Central portion of a broad scale. FIG. 10. Indusia of *Cyathea Tuerckheimii,* normal globose indusium (left) and indusium with scale developed apically (right), *Steyermark 46784,* × 8, US. FIGS. 11–13. Lower epidermis with stomata: 11, *Lophosoria quadripinnata,* superficial stomate near vein (left), others are sunken, *Nisman 92,* × 180, GH. 12, *Metaxya rostrata, Kramer et al. 5651,* × 90, GH. 13, *Cnemidaria dissimilis, Wurdack 34154,* × 90, NY.

SPECIES

I am providing lists of the species under broad geographic headings, as a matter of information and, in many cases, to provide a correct name under the new classification. I have accepted the taxonomy of Holttum for the species of Asia, Malaysia, Australasia and the Pacific, of Tardieu-Blot (1951) for those of Madagascar and (1953) central Africa, and of other current authors for those of the remainder of Africa. I have included only those American species that I believe to be adequately known. They are listed only under the geographic region from which the type originated because, in some cases, their total range is uncertain.

In addition to the synonyms required for the new combinations and new names, others are given when they seem useful. Taxonomic synonyms and the basionyms of *nomina nova* are also given separately, in brackets, alphabetically by the epithet with reference to the correct name.

ACKNOWLEDGEMENTS

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KEY TO GENERA

a. Stem and petioles with trichomes, scales absent, receptacle low, capsule of the sporangium large (ca. 0.4–0.5 mm. long). *b.*

b. Lamina decompound, costa raised, margin of the segments scarely modified, stomates with two subsidiary cells, one on the side of each

guard cell, sunken between the veins, superficial near them (Fig. 11), sporangium stalk with six rows of cells, n=65 ..... 1. *Lophosoria.*

b. Lamina 1-pinnate, costa grooved, margin of pinnae cartillaginous, stomates with three subsidiary cells, one on the side of each guard cell and a third on the side of the smaller one, superficial (Fig. 12) sporangium stalk with four rows of cells, n=ca. 95 ..... 2. *Metaxya.*

a. Stem and petioles with scales, trichomes present or absent on the petioles, stomates with one subsidiary cell, partially enclosing both guard cells, or sometimes with a second one partially enclosing the other, superficial (Fig. 13), receptacle elevated (rarely slightly so), capsule of the sporangium small (ca. 0.15–0.2, rarely to 0.3 mm. long), sporangium stalk with four rows of cells, n=69. *c.*

c. Petiole scales structurally conform (for example Figs. 14–17), the cells of the body similar in orientation, shape, and (usually) in size and color. ..... 3. *Sphaeropteris.*

c. Petiole scales structurally marginate (for example Figs. 23, 27, 29) with a narrow to broad margin of cells different in orientation, size, and (usually) in shape and color from those of the central portion. *d.*

d. Petiole scales (or some of them) with a dark (very rarely lighter colored) apical seta (for example, Fig. 24), similar setae sometimes also borne on the body of the scale (Fig. 37), or on its edge. *e.*

e. Petiole lacking spines, smooth to tuberculate, or with corticinate spines, these mostly conical, a complete, usually caducous, scale perched on top of the spine (Fig. 22), unexpanded croziers lacking spines; scales of the petiole (especially on the abaxial side) more or less appressed, attached at a thickened base or usually at one point of a pseudopeltate or peltate base ..... 4. *Alsophila.*

e. Petiole with squaminate spines, many large, black, mostly obturbinate with a slender apex (Fig. 31), small spines bear the differentiated margins of the scales (Fig. 34), the unexpanded croziers with well developed squaminate spines (Fig. 31), many of them caducous; petiole scales patent, fully adnate or slightly narrowed at the base ..... 5. *Nephelea.*

d. Petiole scales lacking setae, the apex rounded to filamentous (Figs. 40, 41, 46). *f.*

f. Veins free (rarely some branch and rejoin), in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus (Figs. 42–43), costa pubescent above (rarely glabrous), minute indument of the petiole, when present, of squamulae or rarely of patent trichomidia. *g.*

g. Indusium absent ..... 6. *Trichipteris.*

g. Indusium present, rarely scale-like, to sometimes hemitelioid, to usually sphaeropteroid ..... 7. *Cyathea.*

f. Veins forming areolae along the costa (sometimes beyond) (Figs. 49–50), or all free and then in lobed or pinnatifid segments the basal vein on each side connivent to the base of the sinus (Fig. 48) (in parts of the lamina with very deep sinuses sometimes extending above the sinus), costa glabrous above (rarely pubescent), minute indument, when present, of appressed trichomidia, indusium hemitelioid ..... 8. *Cnemidaria.*

1. Lophosoria

Lophosoria Presl, Gefässbündel Stipes der Farrn, 36. 1847 (preprint Abhandl. böhm. Ges. V, **5**:344. 1848). Type: *Lophosoria pruinata* (Sw.) Presl (*Polypodium glaucum* Sw. 1788, not Thunb. 1784, *Polypodium pruinatum* Sw. nom. nov.) = *Lophosoria quadripinnata* (Gmel.) C. Chr.

Trichosorus Liebm. Vid. Selsk. Skr. V, 1:281. 1849. Type: *Alsophila pruinata* (Sw.) Kze. (*Polypodium pruinatum* Sw.) = *Lophosoria quadripinnata* (Gmel.) C. Chr.

I cannot find that the separate publication of Presl's "Gefässbündel" has been accurately dated and therefore accept the date on its title page. Stearn (1954) gives dates for other publications of Presl. Liebmann clearly indicated the type of his genus: "Typus denne Slaegt er *Alsophila pruinata* Kaulf.", although he made no combination for it under *Trichosorus*. At that time a type had not been selected from among the three species originally included in *Lophosoria* by Presl so that although both generic names have the same type, Liebmann's is not superfluous.

An American genus of one species, *Lophosoria quadripinnata* (Gmel.) C. Chr., in the Greater Antilles, Mexico and Central America, Andean South America, south to Bolivia; southern Chile and Juan Fernandez Islands. *Lophosoria* (Fig. 11) is a very distinctive genus and only a selection of its characters is given in the key to genera. Some others are mentioned in the discussion of evolution in the family. A chromosome number of $n=65$ is reported by Walker (1966).

2. Metaxya

Metaxya Presl, Tent. Pterid. 59. 1836. Type: *Metaxya rostrata* (HBK.) Presl (*Polypodium rostratum* Willd. 1810, not Burm. 1768, *Aspidium rostratum* HBK. nom. nov.).

Amphidesmium J. Sm. Ferns Brit. & For. 167. 1866. (Schott, Gen. Fil. sub *Trichopteris*, 1834, nom. nud.; Presl, Tent. Pterid. 246. 1836, nom. nud.; treated as a synonym of *Metaxya* by J. Sm. Lond. Jour. Bot. 1:668. 1842). Type: *Amphidesmium blechnoides* (Hook.) J. Sm. (*Alsophila blechnoides* Hook.) = *Metaxya rostrata* (HBK.) Presl.

Schott's publication of *Amphidesmium* is clearly invalid, although it was generdally accepted by his contemporaries. Presl adopted the genus but supplied so brief a diagnosis that his publication of its name can also be considered to be invalid. If one chooses to accept it as valid, however, then it is important to note that John Smith treated *Amphidesmium* as a synonym of *Metaxya*

a few years later. The name was certainly validly published by John Smith in 1866 and may have been validated earlier.

An American genus of one species, *Metaxya rostrata*, (Fig. 12) in the Lesser Antilles, Central America, northern South America and the Andes south to Bolivia. *Metaxya*, like *Lophosoria*, is a very distinctive genus and only a few of its characters are mentioned in the key to genera. A chromosome number of n=ca. 95 is reported by Roy and Holttum (1965).

3. Sphaeropteris

Sphaeropteris Bernh. Schrad. Jour. Bot. 1800 (2): 122. 1801, not Wall. 1830 (=*Peranema*). Type: *Sphaeropteris medullaris* (Forst.) Bernh. (*Polypodium medullare* Forst).

Schizocaena J. Sm. in Hook. Gen. Fil. t. 2. 1838. Type: *Schizocaena brunonis* J. Sm. = *Sphaeropteris moluccana* (Desv.) Tryon.

Eatoniopteris Bomm. Bull. Soc. Bot. France 20: xix. 1873. Lectotype: *Cyathea insignis* D. C. Eaton (Bommer made no combinations for the names of the 19 species he placed in his new genus) = *Sphaeropteris insignis* (D. C. Eaton) Tryon.

Fourniera Bomm. Bull. Soc. Bot. France 20: xix. 1873. Type: *Fourniera novaecaledoniae* (Mett.) Bomm. (*Alsophila novae-caledoniae* Mett.) = *Sphaeropteris novaecaledoniae* (Mett.) Tryon.

Petiole smooth to tuberculate, or with corticinate spines, sometimes with trichomes; petiole *scales* patent, fully adnate or slightly narrowed at the base, or stipitate, or (especially on the abaxial side) more or less appressed and attached at one point of a somewhat expanded base, structurally conform, the cells of the body all similar in their orientation and shape, and (usually) in their size and color (cilia, teeth or dark setae may be borne on the edge and one or more, usually dark, setae may be borne at the apex); *minute indument* of the petiole, when present, of trichomidia and (or) of squamulae; *costa* pubescent above or rarely glabrous; *veins* free, in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* absent, or present and hemitelioid to sphaeropteroid, or formed of several closely investing scales.

Sphaeropteris (Figs. 5–9, 14–21) is a genus of about 120 species, some 20 of them American and the remainder distributed from India and southeastern Asia to New Zealand, the Marquesas and Pitcairn Island. In the Old World the genus is exactly *Cyathea* subgenus *Sphaeropteris* of Holttum (1963, 1964, 1965). This subgenus was classified by Holttum as follows: section *Sphaeropteris* with subsection *Sphaeropteris* and subsection *Fourniera*, and section *Schizocaena* with subsection *Schizocaena* and subsection *Sacropholis*. In America there are several species, for example, *Sphaeropteris insignis*, S. *Brunei* and S. *horrida* (Fig. 19) that have

the petiole scales very like those of *Sphaeropteris medullaris, S. concinna* (Figs. 20, 21) and other related species of Holttum's subsection *Sphaeropteris*. Other American species do not exhibit relations outside of the western hemisphere. These are represented by a number of rather isolated species or distinctive species-groups that are sufficiently diverse so that, at this time, I hesitate to accommodate them (perhaps as a coordinate section) in Holttum's classification. A chromosome number of $n=69$ was reported by Brownlie (1961) for *Sphaeropteris medullaris* (as *Cyathea medullaris*).

The genus *Sphaeropteris* is characterized by the petiole scales that are structurally conform (undifferentiated or poorly differentiated) in their cellular construction. In most species the cells of the scale (except for processes such as cilia, teeth or dark setae that may be borne on the edge or apex) are nearly alike in their size, color, thickness of walls, their elongate shape and their orientation parallel to the long axis of the scale. Sometimes the cells near the edge are smaller than those at the center, or have thinner walls, or may be much lighter in color. These variations, as well as the various processes that may be borne on the edge or apex, are illustrated in Figs. 14–17 and 20. They are all developed on a basically uniform cellular pattern of the body of the scale. A few species, such as *Sphaeropteris hirsuta* and *S. marginalis,* have some petiole scales slightly marginate with the margin weakly modified and very narrow; others, such as *Sphaeropteris senilis* and *S. stigmosa,* have areas of slightly modified cells occurring at intervals along the margin. These examples of species with tendencies toward a marginate scale nearly provide a connection with *Trichipteris* in which a few species have slightly marginate scales.

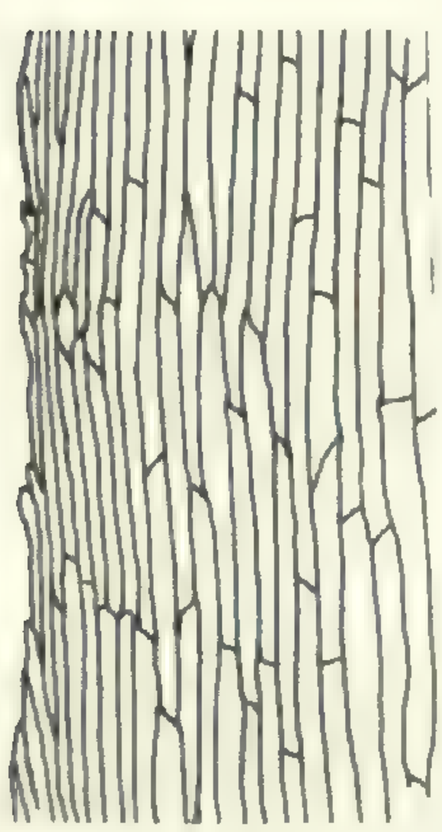
Some species, including the most primitive ones, *Sphaeropteris macarenensis* and *S. mollicula,* lack a dark apical seta on the petiole scale. The others have a dark seta and these include most of the species of *Sphaeropteris* of the paleotropics. However, in *Sphaeropteris albifrons* the seta is nearly concolorous with the brownish scale body; in *S. vittata* it is very small; in *S. discophora* there are two small dark setae at the apex and in *S. agatheti* there are several setulae.

The scales of the species treated by Holttum as subsection *Sacropholis* are much enlarged basally and may be at least 15 cells

thick. The relation to other species of *Sphaeropteris* is clearly indicated by their conform cellular structure, which is most easily seen beyond the thickened basal portion.

Sphaeropteris procera of New Guinea is unique in the genus in having some of the larger scales rather spine-like. These are rigid and subterete basally, while toward the apex the scale body is like that of the smaller scales. They become variously broken with age and are not persistent as definite spines.

The primitive type of indument of the petiole of *Sphaeropteris macarenensis* and S. *mollicula,* which is partly composed of long



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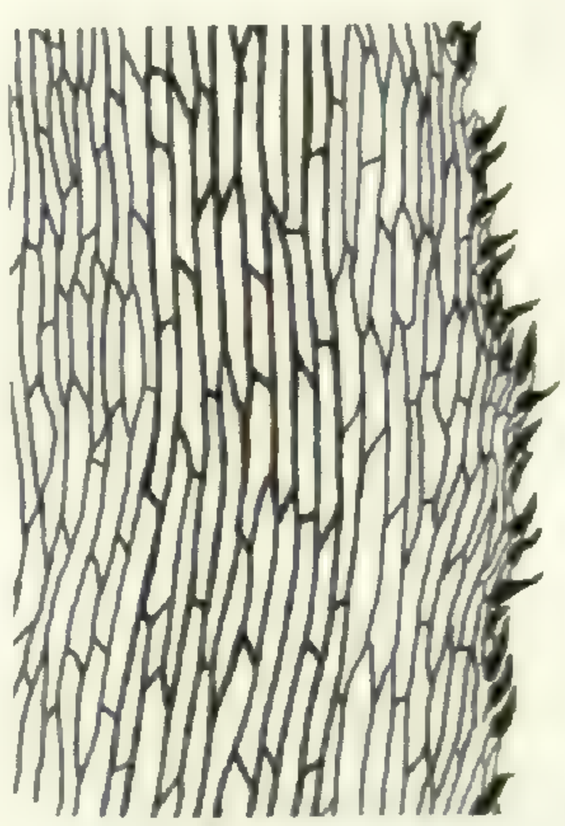

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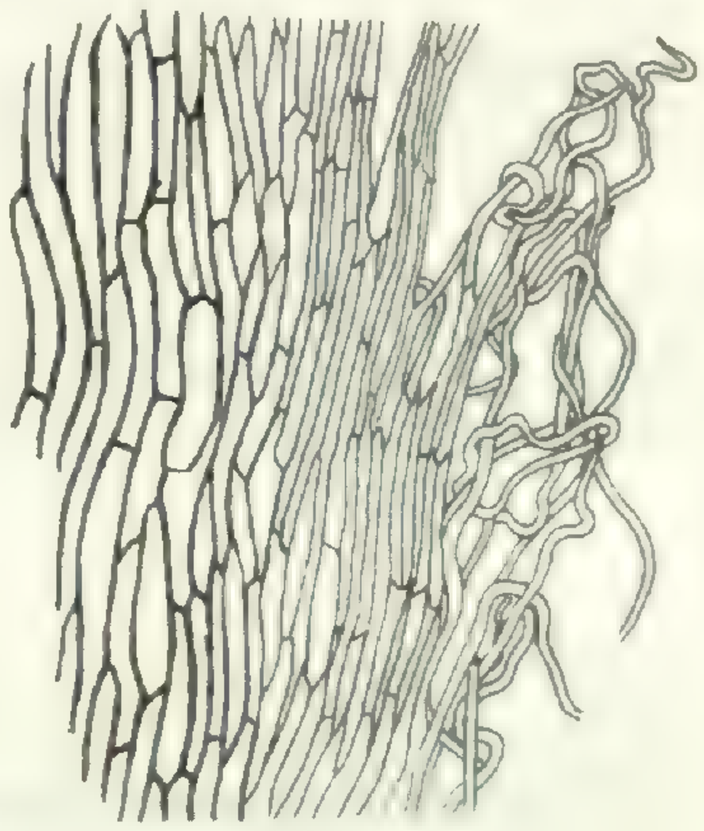

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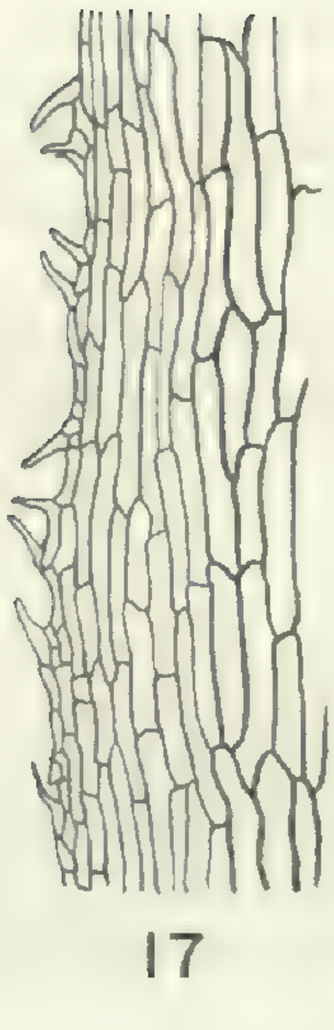

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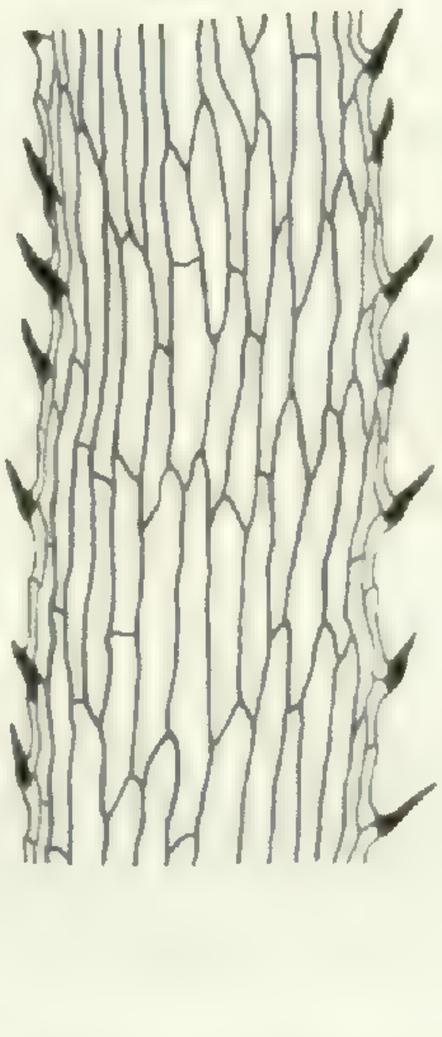

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FIGS. 14–21. SPHAEROPTERIS, portions of petiole scales, all × 30: 14, *S. mollicula, Schultes & Cabrera 13368a,* GH. 15, *Sphaeropteris sp. nov., Schultes 3389,* GH. 16, *S. marginalis, Maguire 24544,* A. 17, *S. myosuroides, Deam 482,* GH. 18, Apex, *S. senilis, Steyermark 91129,* US. 19, Apex, *S. horrida, Morton & Makrinius 2681,* US. 20, *S. concinna, Brass 3724,* GH. 21, Apex, *S. concinna, Brass 3124,* GH.

trichomes, has been discussed in the remarks on evolution. It would be of interest to know whether similar trichomes occur on the stem of these species. I am not able to determine this in the materials available because the persistent petiole bases are so closely crowded that the small areas of stem surface cannot be distinguished with certainty.

WEST INDIES

Sphaeropteris insignis (D. C. Eaton) Tryon, comb. nov., *Cyathea insignis* D. C. Eaton, Mem. Amer. Acad. n.s. 8:215. 1860.

MEXICO AND CENTRAL AMERICA

Sphaeropteris Brunei (Christ) Tryon, comb. nov., *Cyathea Brunei* Christ, Bull. Herb. Boiss. II, 4:947. 1904.

S. myosuroides (Liebm.) Tryon, comb. nov., *Alsophila myosuroides* Liebm. Vid. Selsk. Skr. V, 1:286. 1849.

S. horrida (Liebm.) Tryon, comb. nov., *Cibotium horridum* Liebm. Vid. Selsk. Skr. V, 1:279. 1849, *Cyathea princeps* E. Mayer, Gartenfl. 17:10. 1868.

[*Cyathea princeps*=**Sphaeropteris horrida**].

SOUTH AMERICA

Sphaeropteris aterrima (Hook.) Tryon, comb. nov., *Alsophila aterrima* Hook. Syn. Fil. 38. 1866.

[*Cyathea crassipes*=**Sphaeropteris quindiuensis**].

S. elongata (Hook.) Tryon, comb. nov., *Alsophila elongata* Hook. Sp. Fil. 1:43. 1844.

S. Gardneri (Hook.) Tryon, comb. nov., *Cyathea Gardneri* Hook. Sp. Fil. 1:21. 1844.

S. gibbosa (Kl.) Tryon, comb. nov., *Alsophila gibbosa* Kl. Linnaea 18:542. 1844.

S. hirsuta (Desv.) Tryon, comb. nov., *Polypodium hirsutum* Desv. Ges. Naturf. Freunde Berl. Mag. 5:317. 1811, *Hemitelia hirsuta* (Desv.) Weath.

[*Alsophilia lechria*=**Sphaeropteris mollicula**].

S. macarenensis (Alston) Tryon, comb. nov., *Dryopteris macarenensis* Alston, Mutisia 7:5. 1952, *Alsophila macarenensis* (Alston) Tryon, *Alsophila scopulina* Tryon.

S. macrocarpa (Presl) Tryon, comb. nov., *Hemitelia macrocarpa* Presl, Gefässbündel Stipes der Farrn 41. 1847 (preprint from Abhandl. böhm. Ges. V, 5:352. 1848).

S. marginalis (Kl.) Tryon, comb. nov., *Alsophila marginalis* Kl. Linnaea 18:542. 1844.

S. mollicula (Maxon) Tryon, comb. nov., *Alsophila mollicula* Maxon, Jour. Arn. Arb. 27:440. 1946, *Alsophila lechria* Tryon.

S. quindiuensis (Karst.) Tryon, comb. nov., *Cyathea quindiuensis* Karst. Linnaea 28:454. 1857, *Cyathea crassipes* Sod.

[*Alsophila scopulina*=**Sphaeropteris macarenensis**].

S. senilis (Kl.) Tryon, comb. nov., *Alsophila senilis* Kl. Linnaea 20:442. 1847.

S. stigmosa (Desv.) Tryon, comb. nov., *Hemitelia stigmosa* Desv. Mém. Soc. Linn. Paris 6:321. 1827.

ASIA

Sphaeropteris albosetacea (Bedd.) Tryon, comb. nov., *Alsophila albosetacea* Bedd. Suppl. Ferns So. India Brit. India 2. 1876, *Cyathea albosetacea* (Bedd.) Copel.

S. brunoniana (Hook.) Tryon, comb. nov., *Alsophila brunoniana* Hook. Sp. Fil. 1:52. 1844, *Cyathea brunoniana* (Hook.) Clarke & Baker.

[*Cyathea contaminans*=**Sphaeropteris glauca**].

S. crinita (Hook.) Tryon, comb. nov., *Alsophila crinita* Hook. Icon. Pl. 7: t. 671. 1844, and Sp. Fil. 1:54. 1844, *Cyathea crinita* (Hook.) Copel.

S. glauca (Bl.) Tryon, comb. nov., *Chnoophora glauca* Bl. Enum. Pl. Jav. 243. 1828, *Cyathea contaminans* (Hook.) Copel.

S. hainanensis (Ching) Tryon, comb. nov., *Cyathea hainanensis* Ching, Acta Phytotax. Sinica 8:168. 1959.

S. lepifera (Hook.) Tryon, comb. nov., *Alsophila lepifera* Hook. Sp. Fil. 1:54. 1844, *Cyathea lepifera* (Hook.) Copel.

S. Mertensiana (Kze.) Tryon, comb. nov., *Alsophila Mertensiana* Kze. Bot. Zeit. 6:586. 1848, *Cyathea Mertensiana* (Kze.) Copel.

MALAYSIA

Sphaeropteris aciculosa (Copel.) Tryon, comb. nov., *Cyathea aciculosa* Copel. Phil. Jour. Sci. 60:104. 1936.

S. aeneifolia (vAvR.) Tryon, comb. nov., *Alsophila aeneifolia* vAvR. Nova Guinea 14:3. 1924, *Cyathea aeneifolia* (vAvR.) Copel.

S. agatheti (Holtt.) Tryon, comb. nov., *Cyathea agatheti* Holtt. Kew Bull. 16:51. 1962.

S. albidosquamata (Rosenst.) Tryon, comb. nov., *Cyathea albidosquamata* Rosenst. Fedde Repert. 12:525. 1913. Placed by Holttum (1963) among species that I treat as *Alsophila,* but I believe that it belongs in *Sphaeropteris*.

S. alternans (Hook.) Tryon, comb. nov., *Hemitelia alternans* Hook. Icon. Pl. t. 622. 1844, *Cyathea alternans* (Hook.) Bedd.

S. angiensis (Gepp) Tryon, comb. nov., *Alsophila angiensis* Gepp, in Gibbs, Dutch N. W. New Guinea 69. 1917, *Cyathea angiensis* (Gepp) Domin.

S. angustipinna (Holtt.) Tryon, comb. nov., *Cyathea angustipinna* Holtt. Kew Bull. 16:52. 1962.

S. arthropoda (Copel.) Tryon, comb. nov., *Cyathea arthropoda* Copel. Phil. Jour. Sci. 6 (Bot.): 134. 1911.

S. assimilis (Hook.) Tryon, comb. nov., *Cyathea assimilis* Hook. Syn. Fil. 24. 1865.

S. atrospinosa (Holtt.) Tryon, comb. nov., *Cyathea atrospinosa* Holtt. Kew Bull. 16:52. 1962.

S. atrox (C. Chr.) Tryon, comb. nov., *Cyathea atrox* C. Chr. Brittonia 2:275. 1937.

S. auriculifera (Copel.) Tryon, comb. nov., *Cyathea auriculifera* Copel. Phil Jour. Sci. 6 (Bot.): 364. 1911.

S. binuangensis (vAvR.) Tryon, comb nov., *Cyathea binuangensis* vAvR. Bull. Jard. Bot. Buitenz. III, 2:136. 1920.

S. capitata (Copel.) Tryon, comb. nov., *Cyathea capitata* Copel. Phil. Jour. Sci. 12 (Bot.): 49. 1917.

S. Carrii (Holtt.) Tryon, comb. nov., *Cyathea Carrii* Holtt. Kew Bull. 16:53. 1962.

S. celebica (Bl.) Tryon, comb. nov., *Cyathea celebica* Bl. Enum. Pl. Jav. 245. 1828.

S. concinna (Baker) Tryon, comb. nov., *Alsophila concinna* Baker, Syn. Fil. ed. 2, 459. 1874, *Cyathea sangirensis* (Christ) Copel.

[*Cyathea contaminans*=**Sphaeropteris glauca**].

S. Curranii (Copel.) Tryon, comb. nov., *Cyathea Curranii* Copel. Phil. Jour. Sci. 3:356. 1909.

[*Cyathea deminuens*=**Sphaeropteris parvifolia**].

S. discophora (Holtt.) Tryon, comb. nov., *Cyathea discophora* Holtt. Kew Bull. 16:54. 1962.

S. elliptica (Copel.) Tryon, comb. nov., *Cyathea elliptica* Copel. Phil. Jour. Sci. **12** (Bot.): 51. 1917.

S. Elmeri (Copel.) Tryon, comb. nov., *Alsophila Elmeri* Copel. Leafl. Phil. Bot. 2:419. 1908, *Cyathea Elmeri* (Copel.) Copel.

S. fugax (vAvR.) Tryon, comb. nov., *Cyathea fugax* vAvR. Bull. Jard. Bot. Buitenz. II, 7:8. 1912.

S. fusca (Baker) Tryon, comb. nov., *Cyathea fusca* Baker, in Beccari, Malesia 3: 31. 1886.

S. glauca (Bl.) Tryon (supra).

S. inaequalis (Holtt.) Tryon, comb. nov., *Cyathea inaequalis* Holtt. Kew Bull. 16:56. 1962.

S. insularum (Holtt.) Tryon, comb. nov., *Cyathea insularum* Holtt. Kew Bull. 16:57. 1962.

S. integra (J.Sm.) Tryon, comb. nov., *Cyathea integra* J.Sm. Icon. Pl. t. 638. 1844.

S. Ledermannii (Brause) Tryon, comb. nov., *Hemitelia Ledermannii* Brause, Bot. Jahrb. **56**:60. 1920, *Cyathea macrophylla* Domin.

S. lepifera (Hook.) Tryon (supra).

S. leucotricha (Christ) Tryon, comb. nov., *Cyathea leucotricha* Christ, Ann. Jard. Bot. Buitenz. **20**:135. 1905.

S. lunulata(Forst.) Tryon, comb. nov., *Polypodium lunulatum* Forst. Fl. Ins. Aust. Prod. 83. 1786, *Cyathea lunulata* (Forst.) Copel.

[*Cyathea macrophylla*=**Sphaeropteris Ledermannii**].

S. magna (Copel.) Tryon, comb. nov., *Cyathea magna* Copel. Univ. Calif. Publ. Bot. 18:218. 1942.

S. marginata (Brause) Tryon, comb. nov., *Alsophila marginata* Brause, Bot. Jahrb. **56**:63. 1920, *Cyathea marginata* (Brause) Domin.

S. megalosora (Copel) Tryon, comb. nov., *Cyathea megalosora* Copel. Phil. Jour. Sci. **12** (Bot.): **54**. 1917.

S. moluccana (Desv.) Tryon, comb., nov., *Cyathea moluccana* Desv. Mém. Soc. Linn. Paris 6:322. 1827.

S. Moseleyi (Baker) Tryon, comb. nov., *Cyathea Moseleyi* Baker, Jour. Linn. Soc. Bot. 15:104. 1876.

S. obliqua (Copel.) Tryon, comb. nov., *Cyathea obliqua* Copel. Leafl. Phil. Bot. 4:1150. 1911.

S. obscura (Bedd.) Tryon, comb. nov., *Alsophila obscura* Bedd. Jour. Bot. **25**:321. 1887, *Cyathea obscura* (Bedd.) Copel.

S. papuana (Ridley) Tryon, comb. nov., *Alsophila papuana* Ridley, Trans. Linn. Soc. Lond. II, (Bot.) 9:252. 1916, *Cyathea papuana* (Ridley) vAvR.

S. parvifolia (Holtt.) Tryon, comb. nov., *Alsophila parvifolia* Holtt. Jour. Mal. Br. Roy. As. Soc. 6:19. 1928, *Cyathea deminuens* Holtt.

S. parvipinna (Holtt.) Tryon, comb. nov., *Cyathea parvipinna* Holtt. Kew Bull. 16:60. 1962.

S. persquamulifera (vAvR.) Tryon, comb. nov., *Cyathea contaminans* var. *persquamulifera* vAvR. Bull. Jard. Bot. Buitenz. II, **28**:13. 1918, *Cyathea persquamulifera* (vAvR.) Domin.

S. philippinensis (Baker) Tryon, comb. nov., *Cyathea philippinensis* Baker, Ann. Bot. **5**:186. 1891.

S. pilulifera (Copel.) Tryon, comb. nov., *Cyathea pilulifera* Copel. Univ. Calif. Publ. Bot. **18**:219. 1942.

S. polypoda (Baker) Tryon, comb. nov., *Cyathea polypoda* Baker, Trans. Linn. Soc. Lond. II (Bot.) **4**:250. 1894.

S. procera (Brause) Tryon, comb. nov., *Cyathea procera* Brause, Bot. Jahrb. **56**:50. 1920.

S. pulcherrima (Copel.) Tryon, comb. nov., *Cyathea pulcherrima* Copel. Univ. Calif. Publ. Bot. **18**:219. 1942.

S. Robinsonii (Copel.) Tryon, comb. nov., *Cyathea Robinsonii* Copel. Phil. Jour. Sci. **6** (Bot.): 145. 1911.

S. Rosenstockii (Brause) Tryon, comb. nov., *Cyathea Rosenstockii* Brause, Bot. Jahrb. **56**:49. 1920.

S. runensis (vAvR.) Tryon, comb. nov., *Cyathea runensis* vAvR. Bull. Dépt. Agric. Ind. Néerl. **18**:1. 1908.

[*Cyathea sangirensis*=**Sphaeropteris concinna**].

S. Sarasinorum (Holtt.) Tryon, comb. nov., *Cyathea Sarasinorum* Holtt. Kew Bull. **16**:61. 1962.

S. senex (vAvR.) Tryon, comb. nov., *Cyathea senex* vAvR. Bull. Jard. Bot. Buitenz. II, **16**:4. 1914.

S. setifera (Holtt.) Tryon, comb. nov., *Cyathea setifera* Holtt. Kew Bull. **16**:62. 1962.

S. sibuyanensis (Copel.) Tryon, comb. nov., *Cyathea sibuyanensis* Copel. Leafl. Phil. Bot. **4**:1150. 1911.

S. squamulata (Bl.) Tryon, comb. nov., *Gymnosphaera squamulata* Bl. Enum. Pl. Jav. 243. 1828, *Cyathea squamulata* (Bl.) Copel.

S. stipitipinnula (Holtt.) Tryon, comb. nov., *Cyathea stipitipinnula* Holtt. Kew Bull. **16**:62. 1962.

S. strigosa (Christ) Tryon, comb. nov., *Cyathea strigosa* Christ, Ann. Jard. Bot. Buitenz. **15**:84. 1898.

S. suluensis (Baker) Tryon, comb. nov., *Cyathea suluensis* Baker, Jour. Bot. **17**:65. 1879.

S. tenggerensis (Rosenst.) Tryon, comb. nov., *Alsophila tenggerensis* Rosenst. Medel. Rijksherb. **31**:1. 1917, *Cyathea tenggerensis* (Rosenst.) Domin.

S. Teysmannii (Copel.) Tryon, comb. nov., *Cyathea Teysmannii* Copel. Phil. Jour. Sci. **4** (Bot.): 51. 1909.

S. tomentosa (Bl.) Tryon, comb. nov., *Chnoophora tomentosa* Bl. Enum. Pl. Jav. 244. 1828, *Cyathea tomentosa* (Bl.) Zoll. & Mor.

S. tomentosissima (Copel.) Tryon, comb. nov., *Cyathea tomentosissima* Copel. Univ. Calif. Publ. Bot. **18**:219. 1942.

S. trichodesma (Bedd.) Tryon, comb. nov., *Alsophila trichodesma* Bedd. Jour. Bot. **25**: 321. 1887, *Cyathea trichodesma* (Bedd.) Copel.

S. trichophora (Copel.) Tryon, comb. nov., *Cyathea trichophora* Copel. Phil. Jour. Sci. **6** (Bot.): 363. 1911.

S. tripinnata (Copel.) Tryon, comb. nov., *Cyathea tripinnata* Copel. Phil. Jour. Sci. 1, Suppl. : 251. 1906.

S. tripinnatifida (Roxb.) Tryon, comb. nov., *Cyathea tripinnatifida* Roxb. Calc. Jour. Nat. Hist. **4**:518. 1844.

S. verrucosa (Holtt.) Tryon, comb. nov., *Cyathea verrucosa* Holtt. Kew Bull. **16**:63. 1962.

S. Wallacei (Kuhn) Tryon, comb. nov., *Alsophila Wallacei* Kuhn, Linnaea **36**:153. 1869, *Cyathea Wallacei* (Kuhn) Copel.

S. Werneri (Rosenst.) Tryon, comb. nov., *Cyathea Werneri* Rosenst. Fedde Repert. **5**:34. 1908.

S. Womersleyi (Holtt.) Tryon, comb. nov., *Cyathea Womersleyi* Holtt. Kew Bull. **16**:63. 1962.

S. zamboangana (Copel.) Tryon, comb. nov., *Cyathea zamboangana* Copel. Phil. Jour. Sci. **30**:325. 1926.

AUSTRALIA AND PACIFIC

Sphaeropteris aciculosa (Copel.) Tryon (supra).

S. albifrons (Fourn.) Tryon, comb. nov., *Cyathea albifrons* Fourn. Ann. Sci. Nat. V, **18**:351. 1873.

S. aramaganensis (Kanehira) Tryon, comb. nov., *Cyathea aramaganensis* Kanehira, Bot. Mag. Tokyo **48**:731. 1934.

S. australis (Presl) Tryon, comb. nov., *Hemitelia australis* Presl, Epim. Bot. 33. 1852, *Cyathea Leichardtiana* (F.v.Muell.) Copel.

S. Brackenridgei (Mett.) Tryon, comb. nov., *Cyathea Brackenridgei* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:56. 1863.

[*Cyathea Brownii*=**Sphaeropteris excelsa**].

S. celebica (Bl.) Tryon (supra).

S. Cooperi (F.v.Muell.) Tryon, comb. nov., *Alsophila Cooperi* F.v.Muell. Fragm. Phyt. Austrl. **5**:117. 1866, *Cyathea Cooperi* (F.v.Muell.) Domin.

S. excelsa (Endl.) Tryon, comb. nov., *Alsophila excelsa* Endl. Prod. Fl. Norf. 16. 1833, *Cyathea Brownii* Domin.

S. feani (E. Brown) Tryon, comb. nov., *Cyathea feani* E. Brown, Bishop Mus. Bull. **89**:14. 1931.

S. intermedia (Mett.) Tryon, comb. nov., *Alsophila intermedia* Mett. Ann. Sci. Nat. IV, **15**:83. 1861, *Cyathea intermedia* (Mett.) Copel.

[*Cyathea Leichardtiana*=**Sphaeropteris australis**].

S. leucolepis (Mett.) Tryon, comb. nov., *Cyathea leucolepis* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:56. 1863.

S. lunulata (Forst.) Tryon (supra).

S. medullaris (Forst.) Bernh., *Cyathea medullaris* (Forst.) Sw.

S. microlepidota (Copel.) Tryon, comb. nov., *Cyathea microlepidota* Copel. Jour. Arn. Arb. **30**:435. 1949.

S. nigricans (Mett.) Tryon, comb. nov., *Cyathea nigricans* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:56. 1863.

S. novaecaledoniae (Mett.) Tryon, comb. nov., *Alsophila novae-caledoniae* Mett. Ann. Sci. Nat. IV, **15**:82. 1861, *Cyathea novaecaledoniae* (Mett.) Copel.

S. Parksiae (Copel.) Tryon, comb. nov., *Cyathea Parksiae* Copel. Univ. Calif. Publ. Bot. **12**:377. 1931.

S. propinqua (Mett.) Tryon, comb. nov., *Cyathea propinqua* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:56. 1863.

S. robusta (Watts) Tryon, comb. nov., *Alsophila robusta* Watts, Proc. Linn. Soc. N. S. Wales **39**:261. 1914 (not de Vriese, in Junghuhn, Java, Gestalt Pflanzend. Bauart. 1:310, 476. 1852, nomen nudum), *Cyathea robusta* (Watts) Holtt.

S. samoensis (Brack.) Tryon, comb. nov., *Alsophila samoensis* Brack. U.S.Explor. Exped. **16**:287. 1854, *Cyathea Whitmeei* Baker.

S. subsessilis (Copel.) Tryon, comb. nov., *Cyathea subsessilis* Copel. Phil. Jour. Sci. **6** (Bot.): 359. 1911.

S. truncata (Brack.) Tryon, comb. nov., *Alsophila truncata* Brack. U. S. Explor. Exped. **16**:289. 1854, *Cyathea truncata* (Brack.) Copel.

S. Vaupelii (Copel.) Tryon, comb. nov., *Cyathea Vaupelii* Copel. Phil. Jour. Sci. **6** (Bot.): 360. 1911.

S. vittata (Copel.) Tryon, comb. nov., *Cyathea vittata* Copel. Phil. Jour. Sci. **60**:102. 1936.

[*Cyathea Whitmeei*=**Sphaeropteris samoensis**].

4. Alsophila

Alsophila R. Br. Prod. Fl. Nov. Holl. 158. 1810. Type: *Alsophila australis* R. Br.

Gymnosphaera Bl. Enum. Pl. Jav. 242. 1828. Type: *Gymnosphaera glabra* Bl. = *Alsophila glabra* (Bl.) Hook.

Amphicosmia Gardn. Lond. Jour. Bot. **1**:441. 1842. Lectotype: *Amphicosmia riparia* (Willd.) Gardn. (*Cyathea riparia* Willd.) = *Alsophila capensis* (L. f.) J. Sm.

Dichorexia Presl, Gefässbündel Stipes der Farrn, 36. 1847 (preprint from Abhandl. böhm. Ges. V, **5**:344. 1848). Type: *Dichorexia latebrosa* (Hook.) Presl = *Alsophila latebrosa* Hook.

Thysanobotrya vAvR. Bull. Jard. Bot. Buitenz. II, **28**:66. 1918. Type: *Thysanobotrya arfakensis* (Gepp) vAvR. (*Polybotrya arfakensis* Gepp) = *Alsophila biformis* Rosenst.

Petiole smooth to tuberculate, or with corticinate spines (with squaminate spines in one species), lacking trichomes (in species examined); petiole *scales* (especially on the abaxial side) more or less appressed, attached either at one point of a pseudopeltate to peltate base or at a thickened base (rarely patent and adnate at the thickened base), structurally marginate, with a narrow to broad margin of cells different in orientation, size, shape and usually in color from those of the central portion, some or all scales bearing a dark (rarely lighter colored) seta at the apex and often one seta (or more) on the edge or body of the scale; *minute indument* of the petiole, when present, of trichomidia and (or) squamulae; *costa* usually pubescent above, rarely glabrous; *veins* free, in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* absent, or present and scale-like to sphaeropteroid.

The name *Amphicosmia* might appear to be superfluous because Gardner included *Cyathea multiflora*, the type of *Hemitelia*, in his genus. However, the typification of *Hemitelia* had not been settled at that time and Gardner explicitly considered *Cyathea horrida* to be the type of *Hemitelia*.

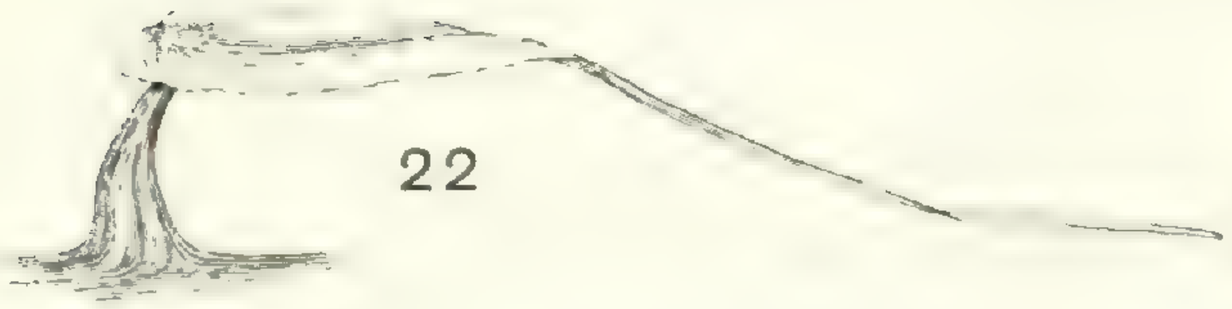
Alsophila (Figs. 22–30) is a pantropic genus of about 230 species, poorly represented in America by about 12 species, well represented in Africa-Madagascar by about 60 species and from India and Ceylon to southern Japan, the Auckland Islands and to the Marquesas by about 160 species. In the paleotropics the

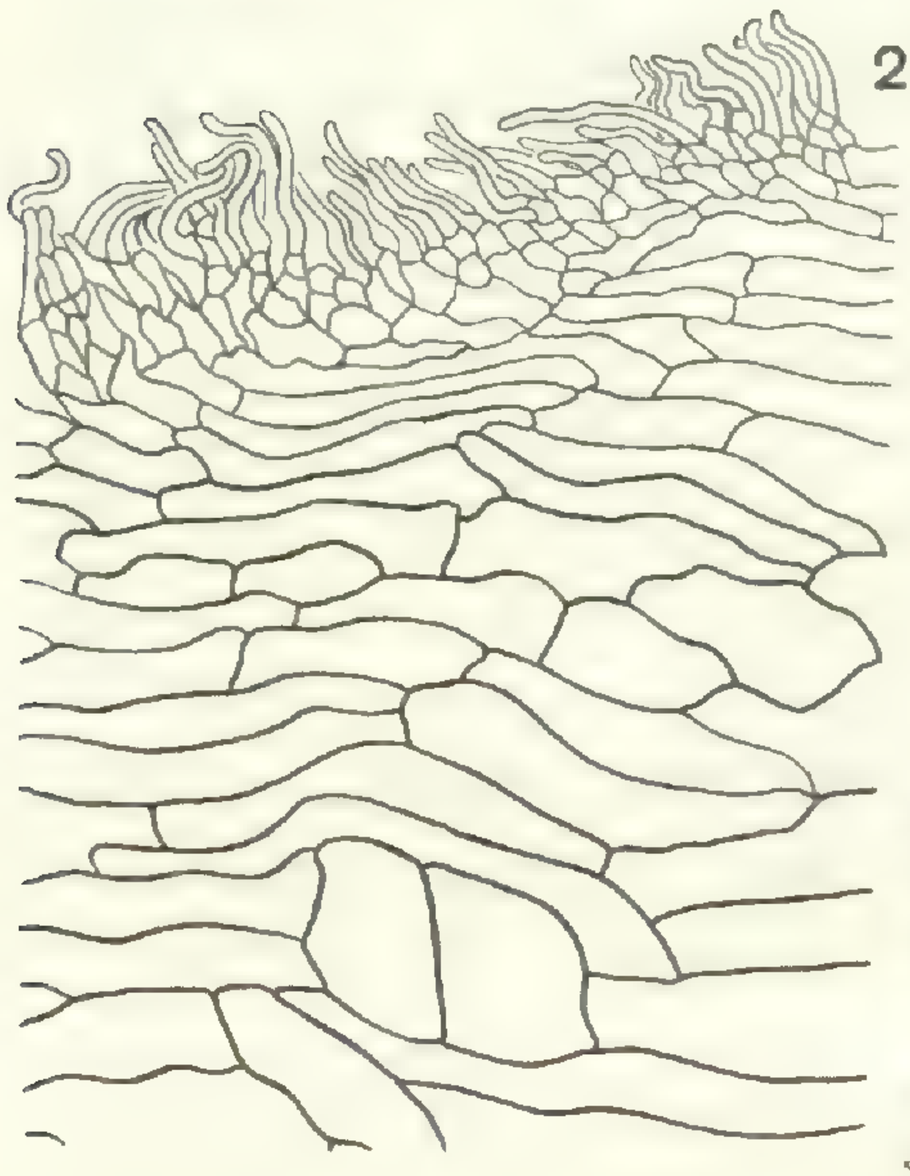
genus is exactly *Cyathea* subgenus *Cyathea* Holttum (1963, 1964, 1965), including section *Cyathea* and section *Gymnosphaera.* Most American species, for example, *A. Brooksii, A. Nockii* and *A. Urbanii,* form a distinct group of indusiate bipinnate species in the Greater Antilles which perhaps has affinities with similar species of Africa and Madagascar. The two other American species, *A. capensis* (also in Africa) and *A. Salvinii,* are evidently related to species of the section *Gymnosphaera.* The size and diversity of *Alsophila* suggest that further studies are desirable to determine the major evolutionary lines within it. A chromosome number of $n=69$ has been reported, for example, in *A. gigantea* (as *Cyathea gigantea*) by Manton and Sledge (1954).

The genus is characterized by its differentiated petiole scales that are marginate and apically setate, and by the petiole spines that (when present) are corticinate (Fig. 22) and arise from the petiole tissue. The cellular differentiation of the petiole scale margin is of two types which are connected by intermediates. One type (Fig. 26), similar to that found in *Nephelea,* has the thin walled marginal cells more or less isodiametric in shape and abruptly distinct from the heavy walled, elongate cells of the central portion of the scale. The other type (Fig. 27) has more elongate marginal cells which gradually differ from the cells of the central portion as they approach the edge of the scale. The scales of *Alsophila Nockii* (Figs. 29, 30) are more or less intermediate between these two types.

All of the species of *Alsophila* that I have seen have an apical seta on some of the petiole scales and, except in a few species of Madagascar, it is dark in color. The seta is more or less concolorous with the brownish scale body in *A. Ballardii, A. bellisquamata, A. Hildebrandtii, A. Hyacinthei* and *A. similis* of Madagascar.

Two further developments in the petiole scales are of interest. One is in *Alsophila Urbanii* of the West Indies, which has small and rather thickened and fleshy petiole scales. They are similar in their texture to some of the species of *Sphaeropteris* having thickened and fleshy scales. The other development is the squaminate spine of *A. auriculata* in Madagascar. The species is similar in this respect to the genus *Nephelea* and, in addition, the stem is spiny as it is in some *Nephelea* species (whether the unexpanded croziers also have spines like *Nephelea* is not known). I believe


22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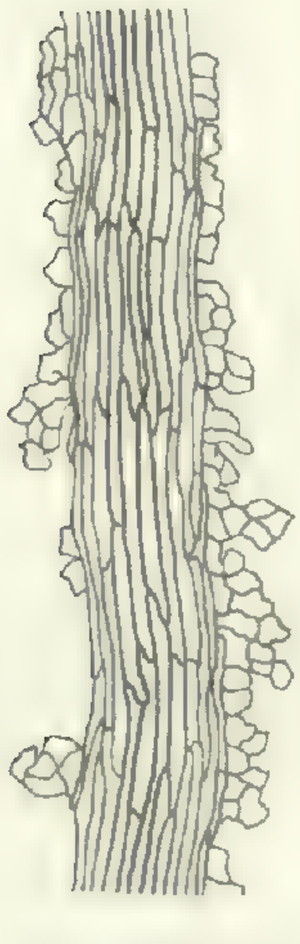
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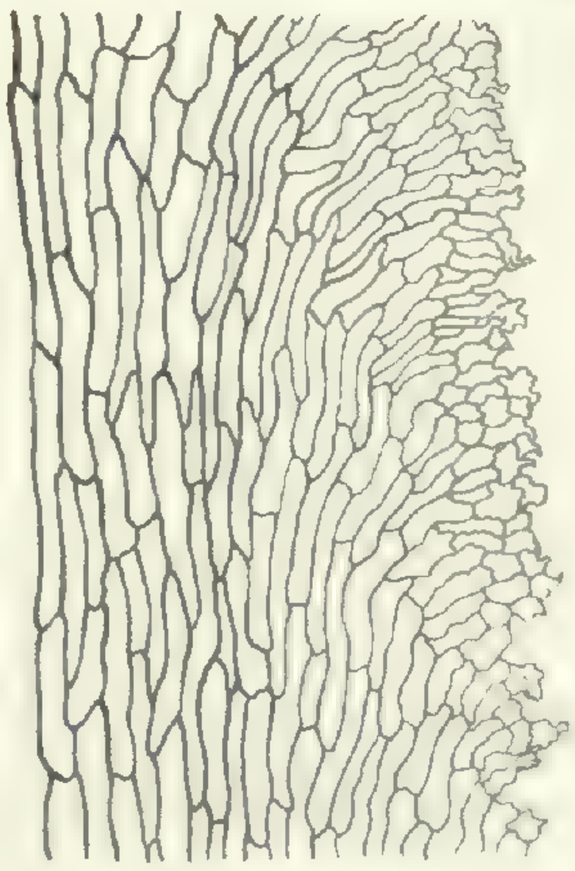
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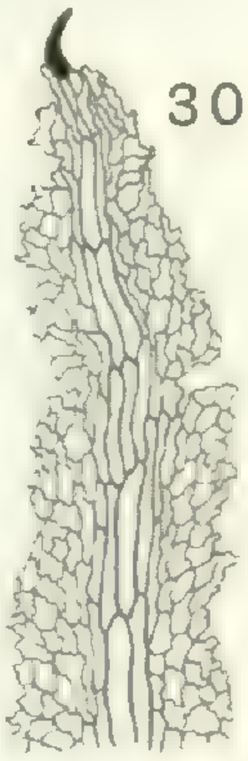
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FIGS. 22–30. ALSOPHILA. FIG. 22. Corticinate petiole spine bearing a scale, *A. Manniana, Goodwin 5,* × 4, GH. FIGS. 23–30. Portions of petiole scales: 23, *A. Manniana, Tryon & Tryon 5626,* × 90, GH. 24, Apex, *A. Manniana* (as in Fig. 23). 25, Apex, *A. capensis,* Brazil, *Leite 3565,* × 150, A. 26, *A. Foersteri, Brass 23382,* × 30, GH. 27, *A. Salvinii, Hernandez X–336,* × 30, US. 28, Apex, *A. Salvinii* (as in Fig. 27). 29, *A. Nockii, Underwood 1355,* × 30, NY. 30, Apex, *A. Nockii* (as in Fig. 29).

that these evolutionary developments in *A. auriculata* are independent of those that led to the squaminate spine in *Nephelea*. Other species of Madagascar show intermediate conditions of variously thickened and rigid scales and I interpret these as evidence for a local origin of the squaminate spines of *A. auriculata*. In *A. albida* the scale base is broad and slightly thickened; in *A. Hildebrandtii* it is thicker; in both the scale is borne on a cortical tubercule. In *A. Melleri* the scale base is quite thick and a cortical tubercule is evidently lacking. In *A. Rolandii* much of the scale is thickened, rigid and rather spine-like; its apical portion is somewhat flattened and its base is borne directly on the petiole. This represents a condition only slightly less extreme than that in *A. auriculata* which has spines. The orientation of the thickened scales changes in this series of species, from a rather appressed one (parallel to the petiole surface) in the first species, *A. albida*, to a patent one in the last, *A. auriculata*. The development of thickened and rigid scales somewhat similar to that of *A. Melleri* and *A. Rolandii* is also seen in *A. Brooksii* and *A. minor* of the West Indies. In these species the specialized scales occur at the very base of the petiole, where it blends into the stem, and in *A. Brooksii* some of the scales are quite spine-like.

One of the notable evolutionary trends in *Alsophila* is the development of aphlebiae. I believe that these are found only in *Alsophila* and, at least in their typical development, only in species that have been placed in the section *Gymnosphaera*. The phyletic significance of this character is not wholly clear and it is possible that aphlebiae have evolved more than once from species with normal leaves. The aphlebiae are typically borne at the very base of the petiole and they form a kind of lacy crown at the stem apex. In some species they are highly dissected and are very different from the normal pinnae (from which they are probably derived). The aphlebiae of *A. capensis* were twice described as new species of *Trichomanes* (*T. incisum* Thunb. and *T. cormophyllum* Kaulf.). Tardieu-Blot (1941) discusses aphlebiae with special reference to the species of Madagascar and presents the various concepts of their nature and origin.

The current literature on African *Cyatheaceae* does not include all of the proposed species and, because of doubt about their taxonomic status, some of these have not been included in the following list.

WEST INDIES

Alsophila Abbottii (Maxon) Tryon, comb. nov., *Cyathea Abbottii* Maxon, Proc. Biol. Soc. Wash. 37:98. 1924.

A. Brooksii (Maxon) Tryon, comb. nov., *Cyathea Brooksii* Maxon, Contrib. U. S. Nat. Herb. 13:24. 1909.

A. confinis (C.Chr.) Tryon, comb. nov., *Cyathea confinis* C.Chr. Kungl. Svensk. Vet.-akad. Handl. III, 16(2):13. 1937.

A. dryopteroides (Maxon) Tryon, comb. nov., *Cyathea dryopteroides* Maxon, Amer. Fern Jour. 14:99. 1925, not *Alsophila dryopteroidea* Brause (=*Thelypteris dryopteroidea* (Brause) Reed), or *Alsophila dryopteridoides* Domin.

A. hotteana (C. Chr. & Ekman) Tryon, comb. nov., *Cyathea hotteana* C.Chr. & Ekman, Kungl. Svensk. Vet.-akad. Handl. III, 16(2):12. 1937.

A. minor (D. C. Eaton) Tryon. comb. nov., *Cyathea minor* D. C. Eaton, Mem. Amer. Acad. n.s., 8:215. 1860.

A. Nockii (Jenm.) Tryon, comb. nov., *Cyathea Nockii* Jenm. Jour. Bot. 17:257. 1879.

A. Urbanii (Brause) Tryon, comb. nov., *Cyathea Urbanii* Brause, in Urban, Symb. Ant. 7:151. 1911.

MEXICO AND CENTRAL AMERICA

Alsophila Salvinii Hook.

SOUTH AMERICA

Alsophila capensis (L.f.) J.Sm. *Hemitelia capensis* (L.f.) Kaulf.

A. Engelii Tryon, nom. nov. for *Cyathea elongata* Karst. Fl. Columb. 2:159 (sub *Cyathea erinacea*), t. 183, f. II, f. 5. 1869 (leg. Engel B!), not *Alsophila elongata* Hook. Sp. Fil. 1:43. 1844.

A. paucifolia Baker, Syn. Fil. ed. 2, 456. 1874.

AFRICA, MADAGASCAR AND INDIAN OCEAN

Alsophila acutula Tryon, nom. nov., for *Cyathea tsaratananensis* Tard. Bull. Soc. Bot. France 88:681. 1941, not C.Chr. 1934.

A. albida (Tard.) Tryon, comb. nov., *Cyathea albida* Tard. Bull. Soc. Bot. France 88:680. 1941.

A. alticola (Tard.) Tryon, comb. nov., *Gymnosphaera alticola* Tard. Naturaliste Malag. 3:76. 1951.

A. andohahelensis Tard. *Gymnosphaera andohahelensis* (Tard.) Tard.

A. appendiculata (Baker) Tryon, comb. nov.. *Cyathea appendiculata* Baker, Jour. Linn. Soc. 15:411. 1876.

A. approximata (Bonap.) Tryon, comb. nov., *Cyathea approximata* Bonap. Notes Ptérid. 5:41. 1917.

A. auriculata (Tard.) Tryon, comb. nov., *Cyathea auriculata* Tard. Naturaliste Malag. 3:75. 1951.

A. Ballardii (Tard.) Tryon, comb. nov., *Cyathea Ballardii* Tard. Naturaliste Malag. 3:75. 1951.

A. bellisquamata (Bonap.) Tryon comb. nov., *Cyathea bellisquamata* Bonap. Notes Ptérid. 16:18. 1925.

A. Boivinii Ettingsh. *Gymnospaera Boivinii* (Ettingsh.) Tard.
[*Cyathea Boivinii*=**Alsophila Hyacinthei**].

A. borbonica (Desv.) Tryon, comb. nov., *Cyathea borbonica* Desv. Ges. Naturf. Freunde Berl. Mag. **5**:328. 1811.

A. camerooniana (Hook.) Tryon, comb. nov., *Cyathea camerooniana* Hook. Syn. Fil. 21. 1865 (not *Alsophila camerunensis* Diels).

A. campanulata Tryon, nom. nov., for *Cyathea Holstii* Hieron. in Engler, Pflanzw. Ost. Afr. C. 88. 1895, not *Alsophila Holstii* Hieron.

A. capensis (L.f.) J.Sm. *Cyathea capensis* (L.f.) Sm.

A. celsa Tryon, nom. nov., for *Cyathea excelsa* Sw. Schrad. Jour. Bot. 1800(2):93. 1801, not *Alsophila excelsa* Endl. 1833.

[*Cyathea costularis*=**Alsophila Rolandii**].

A. Coursii Tard. *Gymnosphaera Coursii* (Tard.) Tard.

A. Deckenii (Kuhn) Tryon, comb. nov., *Cyathea Deckenii* Kuhn, in v. Decken Reis. Ost.-Afr. 3(3)Bot.:57. 1879.

A. decrescens (Kuhn) Tryon, comb. nov., *Cyathea decrescens* Kuhn, Fil. Afr. 164. 1868.

A. Dregei (Kze.) Tryon, comb nov., *Cyathea Dregei* Kze. Linnaea **10**:551. 1836.

[*Cyathea excelsa*=**Alsophila celsa**].

A. glaucifolia Tryon, nom. nov., for *Cyathea glauca* Bory, Voy. Iles Afrique **2**:206. 1804, not *Alsophila glauca* (Bl.) J.Sm. Ferns Brit. & For. 245. 1866.

A. Hildebrandtii (Kuhn) Tryon, comb. nov., *Cyathea Hildebrandtii* Kuhn, Ind. Sem. Hort. Berol. 20. 1875.

[*Cyathea Holstii*=**Alsophila campanulata**].

A. Humbertiana (C.Chr.) Tryon, comb. nov., *Hemitelia Humbertiana* C. Chr. Arch. Bot. (Caen) Bull. Mens. **2**:210. 1928, *Cyathea Humbertiana* (C.Chr.) Diels.

A. Hyacinthei Tryon, nom. nov., for *Cyathea Boivinii* Kuhn, Fil. Afr. 162. 1868, not Ettingsh.. *Cyathea rigidula* Baker, not *Alsophila rigidula* Mart.

A. isaloensis (C.Chr.) Tryon, comb. nov., *Cyathea isaloensis* C.Chr. Dansk. Bot. Ark. **7**:35. 1932.

A. Kirkii (Hook.) Tryon, comb. nov., *Cyathea Kirkii* Hook. Syn. Fil. 22. 1865.

A. Lastii (Baker) Tryon, comb. nov., *Cyathea Lastii* Baker, Jour. Bot. **29**:3. 1891.

A. leptochlamys (Baker) Tryon, comb. nov., *Cyathea leptochlamys* Baker, Jour. Linn. Soc. **22**:535. 1887.

A. ligulata (Baker) Tryon, comb. nov., *Cyathea ligulata* Baker, Jour. Bot. **22**:140. 1884.

A. longipinnata (Bonap.) Tryon, comb. nov., *Cyathea longipinnata* Bonap. Notes Ptérid. **5**:48. 1917.

A. madagascarica Bonap., *Gymnosphaera madagascarica* (Bonap.) Tard.
[*Cyathea madagascarica*=**Alsophila maititanensis**].

A. Manniana (Hook.) Tryon, comb. nov., *Cyathea Manniana* Hook. Syn. Fil. 21. 1865.

A. marattioides (Kaulf.) Tryon, comb. nov.. *Cyathea marattioides* Kaulf. Enum. Fil. 256. 1824.

A. matitanensis Tryon, nom. nov., for *Cyathea madagascarica* Bonap. Notes Ptérid. **5**:49. 1917, not *Alsophila madagascarica* Bonap.

A. melanocaula (Desv.) Tryon, comb. nov., *Cyathea melanocaula* Desv. Mém. Soc. Linn. Paris **6**:322. 1827 (not *Alsophila melanocaulos* vAvR.).

A. melanotricha Tard., *Gymnosphaera melanotricha* (Tard.) Tard.

A. Melleri (Baker) Tryon, comb. nov., *Hemitelia Melleri* Baker, Syn. Fil. ed. 2, 456. 1874, *Gymnosphaera Melleri* (Baker) Tard.

A. Mildbraedii Brause.

A. mossambicensis (Baker) Tryon, comb. nov., *Cyathea mossambicensis* Baker, Ann. Bot. **5**:185. 1891.

A. Nicklesii (Tard. & Ballard) Tryon, comb. nov., *Gymnosphaera Nicklesii* Tard. & Ballard, Not. Syst. **14**:329. 1952.

A. obtusiloba Hook., *Cyathea obtusiloba* (Hook.) Domin.

A. orthogonalis (Bonap.) Tryon, comb. nov.. *Cyathea orthogonalis* Bonap. Notes Ptérid. **5**:32. 1917.

A. Perrieriana (C.Chr.) Tryon, comb. nov., *Cyathea Perrieriana* C.Chr. Dansk Bot. Ark. **7**:19. 1932.

A. pilosula (Tard.) Tryon, comb. nov., *Cyathea pilosula* Tard. Bull. Soc. Bot. France **88**:681. 1941.

A. quadrata (Baker) Tryon, comb. nov., *Cyathea quadrata* Baker, Jour. Linn. Soc. **15**:411. 1876.

[*Cyathea rigidula* Baker=**Alsophila Hyacinthei**].

A. Rolandii Tryon, nom. nov., for *Cyathea costularis* Roland Bonap. Notes Ptérid. **5**:44. 1917, not *Alsophila costularis* Baker.

A. Schliebenii Reim.

[*Cyathea Schliebenii*=**Alsophila tanzaniana**].

A. sechellarum (Mett.) Tryon, comb. nov., *Cyathea sechellarum* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:58. 1863.

A. serratifolia (Baker) Tryon, comb. nov., *Cyathea serratifolia* Baker, Jour. Bot. **22**:139. 1884.

A. similis (C.Chr.) Tryon, comb. nov., *Cyathea similis* C.Chr. Ind. Fil. 195. 1905, nom. nov. for *Cyathea discolor* Baker, not Bory.

A. Stuhlmannii (Hieron.) Tryon, comb. nov., *Cyathea Stuhlmannii* Hieron. Bot. Jahrb. **28**:340. 1900.

A. tanzaniana Tryon, nom. nov.. for *Cyathea Schliebenii* Reim. Notizbl. Bot. Gart. Berlin **11**:916, 1933, not *Alsophila Schliebenii* Reim.

A. Thomsonii (Baker) Tryon, comb. nov., *Cyathea Thomsonii* Baker, Jour. Bot. **19**:180. 1881.

A. tsaratananensis (C.Chr.) Tryon, comb. nov., *Cyathea tsaratananensis* C.Chr. Ind. Fil. Suppl. 3:64. 1934, nom. nov. for *Cyathea subincisa* C.Chr., not (Kze.) Domin.

[*Cyathea tsaratananensis* Tard.=**Alsophila acutula**].

A. tsilotsilensis (Tard.) Tryon, comb. nov., *Cyathea tsilotsilensis* Tard. Bull. Soc. Bot. France **88**:682. 1941.

A. Viguieri (Tard.) Tryon, comb. nov., *Cyathea Viguieri* Tard. Bull. Soc. Bot. France **88**: 682. 1941.

A. Welwitschii (Hook.) Tryon, comb. nov., *Cyathea Welwitschii* Hook. Syn. Fil, 21. 1865.

A. zakamenensis (Tard.) Tryon, comb. nov., *Cyathea zakamenensis* Tard. Bull. Soc. Bot. France **88**:683. 1941.

ASIA

Alsophila Andersonii Bedd. *Cyathea Andersonii* (Bedd.) Copel.

A. borneensis (Copel.) Tryon, comb. nov., *Cyathea borneensis* Copel. Phil. Jour. Sci. **6** (Bot.): 135. 1911.

[*Cyathea chinensis*=**Alsophila costularis**].

A. costularis Baker, *Cyathea chinensis* Copel.

A. denticulata Baker, *Cyathea Hancockii* Copel.
A. gigantea Hook. *Cyathea gigantea* (Hook.) Copel.
[*Cyathea Hancockii*=**Alsophila denticulata**].
A. Henryi Baker, *Cyathea Henryi* (Baker) Copel.
A. Hookeri (Thwaites) Tryon, comb. nov., *Cyathea Hookeri* Thwaites, Enum. Pl. Zeylan. 396. 1864.
A. khasyana Kuhn, *Cyathea khasyana* (Kuhn) Diels.
A. latebrosa Hook. *Cyathea latebrosa* (Hook.) Copel.
A. Loheri (Christ) Tryon, comb. nov., *Cyathea Loheri* Christ, Bull. Herb. Boiss. II, 6:1007. 1906.
A. Metteniana Hance, *Cyathea Metteniana* (Hance), C.Chr. & Tard.
A. nilgirensis (Holtt.) Tryon, comb. nov., *Cyathea nilgirensis* Holtt. Kew Bull. 19:468. 1965.
A. Ogurae Hayata, *Cyathea Ogurae* (Hayata) Domin.
A. podophylla Hook. *Cyathea podophylla* (Hook.) Copel.
A. Salletii (Tard. & C.Chr.) Tryon, comb. nov., *Cyathea Salletii* Tard. & C.Chr. Bull. Mus. Hist. Nat. Paris. II, 6:450. 1934.
A. sinuata (Hook. & Grev.) Tryon, comb. nov., *Cyathea sinuata* Hook. & Grev. Icon. Fil. t. 106. 1828.
A. spinulosa (Hook.) Tryon, comb. nov., *Cyathea spinulosa* Hook. Sp. Fil. 1:25. 1844.
A. Walkerae (Hook.) J.Sm. *Cyathea Walkerae* Hook.

MALAYSIA

Alsophila acanthophora (Holtt.) Tryon, comb. nov., *Cyathea acanthophora* Holtt. Kew Bull. 16:51. 1962.
A. acrostichoides vAvR., *Cyathea acrostichoides* (vAvR.) Domin.
A. acuminata (Copel) Tryon, comb. nov., *Cyathea acuminata* Copel. Phil. Jour. Sci. 81:15. 1952, (*Alsophila acuminata* J.Sm. Lond. Jour. Bot. 1:667. 1842 is a nomen nudum).
A. Alderwereltii (Copel.) Tryon, comb. nov., *Cyathea Alderwereltii* Copel. Phil. Jour. Sci. 4 (Bot): 50. 1909, nom. nov. for *Hemitelia sumatrana* vAvR., not *Cyathea sumatrana*. Baker
A. Alleniae (Holtt.) Tryon, comb. nov., *Cyathea Alleniae* Holtt. Kew Bull. 16:52. 1962.
A. alpina vAvR., *Cyathea trachypoda* vAvR.
A. amboinensis vAvR., *Cyathea amboinensis* (vAvR.) Merrill.
A. Annae vAvR., *Cyathea Annae* (vAvR.) Domin.
A. apiculata Rosenst., *Cyathea apiculata* (Rosenst.) Domin.
A. apoensis (Copel.) Tryon. comb. nov., *Cyathea apoensis* Copel. Leafl. Phil. Bot. 3:802. 1910.
A. Archboldii (C.Chr.) Tryon, comb. nov., *Cyathea Archboldii* C.Chr. Brittonia 2:278. 1937.
A. arfakensis Gepp, *Cyathea Kanehirae* Holtt.
[*Cyathea arfakensis*=**Alsophila Lilianiae**].
[*Cyathea ascendens*=**Alsophila Rosenstockii**].
A. atropurpurea (Copel.) C.Chr., *Cyathea atropurpurea* Copel.
A. batjanensis Christ, *Cyathea batjanensis* (Christ) Copel.
A. biformis Rosenst. *Stenochlaena dubia* vAvR., not *Alsophila dubia* Bedd., *Cyathea biformis* (Rosenst.) Copel.
A. borneensis (Copel.) Tryon (supra).

A. Brausei Tryon, nom. nov., for *Cyathea Hunsteiniana* Brause, Bot. Jahrb. **56**:58. 1920, not *Alsophila Hunsteiniana* Brause.

A. Buennemeijeri (vAvR.) Tryon, comb. nov., *Cyathea Buennemeijeri* vAvR. Bull. Jard. Bot. Buitenz. III, **5**:187. 1922.

A. callosa (Christ) Tryon, comb. nov., *Cyathea callosa* Christ, Bull. Herb. Boiss. II, **6**:1008. 1906.

A. catillifera (Holtt.) Tryon, comb. nov., *Cyathea catillifera* Holtt. Kew Bull. **16**:53. 1962.

A. caudata Hook. *Cyathea caudata* (Hook.) Copel.

[*Cyathea Christii*=**Alsophila Hermannii**].

A. cincinnata (Brause) Tryon, comb. nov., *Cyathea cincinnata* Brause, Bot. Jahrb. **56**:52. 1920.

A. cinerea(Copel.) Tryon, comb. nov., *Cyathea cinerea* Copel. Leafl. Phil. Bot. **5**:1681. 1913.

A. coactilis (Holtt.) Tryon, comb. nov., *Cyathea coactilis* Holtt. Blumea **11**:533. 1962.

A. commutata Mett. *Cyathea recommutata* Copel.

A. costalisora (Copel.) Tryon, comb. nov., *Cyathea costalisora* Copel. Univ. Calif. Publ. Bot. **18**:218. 1942.

[*Cyathea costulisora*=**Alsophila montana**].

A. crassicaula Tryon, nom. nov., for *Cyathea Ledermannii* Brause, Bot. Jahrb. **56**:56. 1920, not *Alsophila Ledermannii* Brause.

A. crenulata (Mett.) Hook. *Cyathea Raciborskii* Copel.

[*Cyathea crenulata*=**Alsophila polycarpa**].

A. cucullifera (Holtt.) Tryon, comb. nov., *Cyathea cucullifera* Holtt. Kew Bull. **16**:54. 1962.

A. dicksonioides (Holtt.) Tryon, comb. nov., *Cyathea dicksonioides* Holtt. Blumea **11**:529. 1962.

A. dimorpha Christ, *Cyathea dimorpha* (Christ) Copel.

A. Doctersii (vAvR.) Tryon, comb. nov., *Cyathea Doctersii* vAvR. Bull. Jard. Bot. Buitenz. III, **2**:136. 1920.

A. Edanoi (Copel.) Tryon, comb. nov., *Cyathea Edanoi* Copel. Phil. Jour. Sci. **46**:211. 1931.

A. eriophora (Holtt.) Tryon, comb. nov., *Cyathea eriophora* Holtt. Kew Bull. **16**:55. 1962.

A. everta (Copel.) Tryon, comb. nov., *Cyathea everta* Copel. Univ. Calif. Publ. Bot. **18**:218. 1942.

A. excavata (Holtt.) Tryon. comb. nov., *Cyathea excavata* Holtt. Gard. Bull. Str. Sett. **8**:306. 1935.

A. Fenicis (Copel.) C.Chr. *Cyathea Fenicis* Copel.

A. ferruginea (Christ) Tryon, comb. nov., *Cyathea ferruginea* Christ, Phil. Jour. Sci. **2** (Bot.): 181. 1907.

A. Foersteri (Rosenst.) Tryon, comb. nov., *Cyathea Foersteri* Rosenst. Fedde Repert. **10**:321. 1912.

A. fuliginosa Christ, *Cyathea fuliginosa* (Christ) Copel.

A. geluensis (Rosenst.) Tryon, comb. nov., *Cyathea geluensis* Rosenst. Fedde Repert. **5**:371. 1908.

A. gigantea Hook. *Cyathea gigantea* (Hook.) Holtt.

A. glabra (Bl.) Hook. *Cyathea glabra* (Bl.) Copel.

A. glaberrima (Holtt.) Tryon, comb. nov., *Cyathea glaberrima* Holtt. Kew Bull. **16**:55. 1962.

A. gleichenioides (C.Chr.) Tryon, comb. nov., *Cyathea gleichenioides* C.Chr. Brittonia **2**:281. 1937.

A. gregaria Brause, *Cyathea gregaria* (Brause) Domin.

A. halconensis (Christ) Tryon, comb. nov., *Cyathea halconensis* Christ, Phil. Jour. Sci. 3 (Bot.): 270. 1908.

A. Havilandii (Baker) Tryon, comb. nov., *Cyathea Havilandii* Baker, Trans. Linn. Soc. Lond. II, (Bot.) 4:249. 1894.

A. Hermannii Tryon, nom. nov., for *Cyathea Christii* Copel. Phil. Jour. Sci. 1, Suppl. II: 144. 1906, not *Alsophila Christii* Sod.

A. heterochlamydea (Copel.) Tryon, comb. nov., *Cyathea heterochlamydea* Copel. Leafl. Phil. Bot. 2:418. 1908.

A. Hooglandii (Holtt.) Tryon, comb. nov., *Cyathea Hooglandii* Holtt. Kew Bull. 16:56. 1962.

A. Hornei Baker, *Cyathea Hornei* (Baker) Copel.

A. horridula (Copel.) Tryon, comb. nov., *Cyathea horridula* Copel. Univ. Calif. Publ. Bot. 18:219. 1942.

[*Cyathea Hunsteiniana*=**Alsophila Brausei**].

A. hymenodes (Mett.) Tryon, comb. nov., *Cyathea hymenodes* Mett. Ann. Mus. Bot. Lugd.-Bat. 1:57. 1863.

A. imbricata (vAvR.) Tryon, comb. nov., *Cyathea imbricata* vAvR. Nova Guinea 14:11. 1924.

A. incisoserrata (Copel) C.Chr. *Cyathea incisoserrata* Copel.

A. inquinans (Christ) Tryon, comb. nov., *Cyathea inquinans* Christ, Verhandl. Naturf. Ges. Basel 11:422. 1896.

A. insulana (Holtt.) Tryon, comb. nov., *Cyathea insulana* Holtt. Kew Bull. 16:56, 1962.

A. javanica (Bl.) Tryon, comb. nov., *Cyathea javanica* Bl. Enum. Pl. Jav. 245. 1828.

A. Junghuhniana Kze. *Cyathea Junghuhniana* (Kze.) Copel.

[*Cyathea Kanehirae*=**Alsophila arfakensis**].

A. Klossii (Ridley) Tryon, comb. nov., *Cyathea Klossii* Ridley, Trans. Linn. Soc. II (Bot.) 9:251. 1916.

A. latebrosa Hook. *Cyathea latebrosa* (Hook.) Copel.

A. latipinnula (Copel.) Tryon, comb. nov., *Cyathea latipinnula* Copel. Leafl. Phil. Bot. 4:1149. 1911.

[*Cyathea Ledermannii*=**Alsophila crassicaula**].

A. lepidoclada Christ, *Cyathea lepidoclada* (Christ) Domin.

A. Lilianiae Tryon, nom. nov., for *Cyathea arfakensis* Gepp, in Lilian S. Gibbs, Dutch N.W. New Guinea 69. 1917, not *Alsophila arfakensis* Gepp.

A. Loerzingii (Holtt.) Tryon, comb. nov., *Cyathea Loerzingii* Holtt. Kew Bull. 16:58. 1962.

A. Loheri (Christ) Tryon (supra).

A. longipes (Copel.) Tryon, comb. nov., *Cyathea longipes* Copel. Phil. Jour. Sci. 12 (Bot.): 54. 1917.

A. lurida (Bl.) Hook. *Cyathea lurida* (Bl.) Copel.

A. Macgillivrayi Baker, *Cyathea Macgillivrayi* (Baker) Diels.

A. Macgregorii (F. v. Muell.) Tryon, comb. nov., *Cyathea Macgregorii* F. v. Muell. Trans. Roy. Soc. Victoria 1(2):40. 1889.

A. macropoda (Domin) Tryon, comb. nov., *Cyathea macropoda* Domin, Acta Bot. Bohem. 9:133, 1930, nom. nov. for *Cyathea longipes* vAvR., not Copel.

A. magnifolia (vAvR.) Tryon, comb. nov., *Cyathea magnifolia* vAvR. Bull. Jard. Bot. Buitenz. III, 2:135. 1920.

A. masapilidensis (Copel.) Tryon, comb. nov., *Cyathea masapilidensis* Copel. Phil. Jour. Sci. 81:17. 1952.

A. media (Wagn. & Greth.) Tryon, comb. nov., *Cyathea media* Wagn. & Greth. Univ. Calif. Publ. Bot. **23**:44. 1948.

A. mesosora (Holtt.) Tryon, comb. nov., *Cyathea mesosora* Holtt. Kew Bull. **16**:57. 1962. Placed by Holttum (1963) among species of *Sphaeropteris*, but I believe that it belongs in *Alsophila*.

A. micra Tryon, nom. nov., for *Cyathea parva* Copel. Univ. Calif. Publ. Bot. **18**:219. 1942, not *Alsophila parva* Maxon.

A. microchlamys (Holtt.) Tryon, comb. nov., *Cyathea microchlamys* Holtt. Kew Bull. **16**:58. 1962.

A. microphylloides (Rosenst.) Tryon, comb. nov., *Cyathea microphylloides* Rosenst. Fedde Repert. **12**:164. 1913.

A. modesta Baker, *Cyathea modesta* (Baker) Copel.

A. montana (vAvR.) Tryon, comb. nov., *Hemitelia montana* vAvR. Bull. Jard. Bot. Buitenz. III, **2**:153. 1920, *Cyathea costulisora* Domin.

A. Muelleri (Baker) Tryon, comb. nov., *Cyathea Muelleri* Baker, Jour. Bot. **28**:104. 1890.

A. negrosiana (Christ) Tryon, comb. nov., *Cyathea negrosiana* Christ, Phil. Jour. Sci. **2** (Bot.): 181. 1907.

A. nigrolineata (Holtt.) Tryon, comb. nov., *Cyathea nigrolineata* Holtt. Kew Bull. **16**:58. 1962.

A. nigropaleata (Holtt.) Tryon. comb. nov., *Cyathea nigropaleata* Holtt. Kew Bull. **16**:59. 1962.

A. oinops (Hassk.) Tryon, comb. nov., *Cyathea oinops* Hassk. Jour. Bot. Hook. Kew Gard. Misc. **7**:322. 1855.

A. oosora (Holtt.) Tryon, comb. nov., *Cyathea oosora* Holtt. Kew Bull. **16**:59. 1962.

A. orientalis (Kze.) Tryon, comb. nov., *Disphenia orientalis* Kze. Bot. Zeit. **6**:283. 1848, *Cyathea orientalis* (Kze.) Moore.

A. pachyrrhachis (Copel.) Tryon, comb. nov., *Cyathea pachyrrhachis* Copel. Univ. Calif. Publ. Bot. **18**:218. 1942.

A. pallidipaleata (Holtt.) Tryon, comb. nov., *Cyathea pallidipaleata* Holtt. Kew Bull. **16**:60. 1962.

[*Cyathea parva*=**Alsophila micra**].

A. patellifera (vAvR.) Tryon, comb. nov., *Cyathea patellifera* vAvR. Bull. Jard. Bot. Buitenz. **II, 16**:4. 1914.

A. percrassa (C.Chr.) Tryon, comb. nov., *Cyathea percrassa* C.Chr. Brittonia **2**:279. 1937.

A. perpelvigera (vAvR.) Tryon, comb. nov., *Cyathea perpelvigera* vAvR. Nova Guinea **14**:11. 1924.

A. perpunctulata (vAvR.) Tryon, comb. nov., *Hemitelia perpunctulata* vAvR. Bull. Jard. Bot. Buitenz. **II, 28**:25. 1918, *Cyathea perpunctulata* (vAvR.) Domin.

A. physolepidota (Alston) Tryon, comb. nov., *Cyathea physolepidota* Alston, Nova Guinea n.s. **7**:1. 1956.

A. polycarpa (Jungh.) Tryon, comb. nov., *Cyathea polycarpa* Jungh. Nat. Geneesk. Arch. Neerl. Ind. **2**:40. 1845, *Cyathea crenulata* Bl., not *Alsophila crenulata* (Mett.) Hook.

A. pruinosa (Rosenst.) Tryon, comb. nov., *Cyathea pruinosa* Rosenst. Fedde Repert. **12**:163. 1913.

A. pseudomuelleri (Holtt.) Tryon, comb. nov., *Cyathea pseudomuelleri* Holtt. Kew Bull. **16**:61. 1962.

A. punctulata vAvR. *Cyathea punctulata* (vAvR.) vAvR.

A. pycnoneura (Holtt.) Tryon, comb. nov., *Cyathea pycnoneura* Holtt. Blumea **11**:533. 1962.

[*Cyathea Raciborskii*=**Alsophila crenulata**].
A. ramispina Hook. *Cyathea ramispina* (Hook.) Copel.
A. Rebeccae F. v. Muell. *Cyathea Rebeccae* (F. v. Muell.) Domin.
[*Cyathea recommutata*=**Alsophila commutata**].
A. recurvata Brause, *Cyathea recurvata* (Brause) Domin.
A. rigens (Rosenst.) Tryon, comb. nov., *Cyathea rigens* Rosenst. Fedde Repert. **12**:163. 1913.
A. Rosenstockii Brause, *Cyathea ascendens* Domin.
A. rubella (Holtt.) Tryon, comb. nov., *Cyathea rubella* Holtt. Kew Bull. **16**:61. 1962.
A. rubiginosa Brause, *Cyathea rubiginosa* (Brause) Domin.
A. rufopannosa (Christ) Tryon, comb. nov., *Cyathea rufopannosa* Christ, Phil. Jour. Sci. **2** (Bot.): 180. 1907.
A. saccata (Christ) Tryon, comb. nov., *Cyathea saccata* Christ, Ann. Jard. Bot. Buitenz. II, **4**:42. 1904.
A. scandens Brause, *Cyathea scandens* (Brause) Domin.
A. Schlechteri Brause, *Cyathea Schlechteri* (Brause) Domin.
A. semiamplectens (Holtt.) Tryon, comb. nov., *Cyathea semiamplectens* Holtt. Kew Bull. **16**:62. 1962.
A. setulosa (Copel.) Tryon, comb. nov., *Cyathea setulosa* Copel. Phil. Jour. Sci. **81**:14. 1952.
A. subtripinnata (Holtt.) Tryon, comb. nov., *Cyathea subtripinnata* Holtt. Blumea **11**:534. 1962.
A. sumatrana (Baker) Tryon, comb. nov., *Cyathea sumatrana* Baker, Jour. Bot. **18**:209. 1880.
A. tenuis Brause, *Cyathea tenuicaulis* Domin.
A. ternatea (vAvR.) Tryon, comb. nov., *Cyathea ternatea* vAvR. Bull. Jard. Bot. Buitenz. III, **5**:191. 1922.
[*Cyathea trachypoda*=**Alsophila alpina**].
A. Vandeusenii (Holtt.) Tryon, comb. nov., *Cyathea Vandeusenii* Holtt. Blumea **11**:529. 1962.
A. wengiensis Brause, *Cyathea wengiensis* (Brause) Domin.

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[*Cyathea affinis*=**Alsophila tahitensis**].
Alsophila alata Fourn. *Cyathea alata* (Fourn.) Copel.
A. alta (Copel.) Tryon, comb. nov., *Cyathea alta* Copel. Phil. Jour. Sci. **60**:104. 1936.
A. aneitensis (Hook.) Tryon, comb. nov., *Cyathea aneitensis* Hook. Syn. Fil. 26. 1865.
A. Archboldii (C.Chr.) Tryon (supra).
A. australis R.Br. *Cyathea australis* (R.Br.) Domin.
A. Baileyana Domin, *Cyathea Baileyana* (Domin) Domin.
A. brevipinna (Benth.) Tryon, comb. nov., *Cyathea brevipinna* Benth. Fl. Austral. 7:709. 1878.
A. cicatricosa (Holtt.) Tryon, comb. nov., *Cyathea cicatricosa* Holtt. Blumea **12**:274. 1964.
A. Colensoi Hook. f. *Cyathea Colensoi* (Hook. f.) Domin.
A. Cunninghamii (Hook. f.) Tryon, comb. nov., *Cyathea Cunninghamii* Hook. f. Icon. Pl. t. 985. 1854.
[*Cyathea dealbata*=**Alsophila tricolor**].
A. decurrens Hook. *Cyathea decurrens* (Hook.) Copel.

A. Ferdinandii Tryon, nom. nov., for *Hemitelia Macarthurii* F. v. Muell. Fragm. Phyt. Austral. 8:176. 1874, *Cyathea Macarthurii* (F. v. Muell.) Baker, not *Alsophila Macarthurii Hook. Cyathea Moorei* Baker, not *Alsophila Moorei* J.Sm.

A. Hornei Baker (supra).

A. kermadecensis (Oliver) Tryon, comb. nov., *Cyathea kermadecensis* Oliver, Trans. N. Z. Instit. **42**:158. 1910.

[*Cyathea Macarthurii*=**Alsophila Ferdinandii**].

A. marcescens (N.A.Wakef.) Tryon, comb. nov., *Cyathea marcescens* N.A.Wakef. Victoria Nat. **59**:33. 1942.

A. Milnei (Hook. f.) Tryon, comb. nov., *Cyathea Milnei* Hook. f. Handb. Fl. New Zeal. 349. 1864.

A. plagiostegia (Copel.) Tryon, comb. nov., *Cyathea plagiostegia* Copel. Bishop Mus. Bull. **59**:9. 1929.

A. Rebeccae F. v. Muell. *Cyathea Rebeccae* (F. v. Muell.) Domin.

A. Robertsiana F. v. Muell. *Cyathea Robertsiana* (F. v. Muell.) Domin.

A. Smithii (Hook. f.) Tryon, comb. nov., *Cyathea Smithii* Hook. f. Fl. New Zeal. **2**:8. 1854.

A. solomonensis (Holtt.) Tryon, comb. nov., *Cyathea solomonensis* Holtt. Blumea **12**:252. 1964.

A. stelligera (Holtt.) Tryon, comb. nov., *Cyathea stelligera* Holtt. Blumea **12**:250. 1964.

A. Stokesii (E. Brown) Tryon, comb. nov., *Cyathea Stokesii* E. Brown, Bishop Mus. Bull. **89**:16. 1931.

A. tahitensis Brack. *Cyathea affinis* (Forst.) Sw., not *Alsophila affinis* (Presl) Fée.

A. tricolor (Colenso) Tryon, comb. nov., *Cyathea tricolor* Colenso, Trans. New Zeal. Instit. **15**:304. 1883, *Cyathea dealbata* (Forst.) Sw., not *Alsophila dealbata* Presl.

A. Vieillardii (Mett.) Tryon, comb. nov., *Cyathea Vieillardii* Mett. Ann. Sci. Nat. IV, **15**:82. 1861.

A. Woollsiana F. v. Muell. *Cyathea Woollsiana* (F. v. Muell.) Domin.

5. Nephelea

Nephelea, genus novum Cyatheacearum petiolis crosieribusque spinis squaminatis magnis atris et squamis cellulose marginatis setam atratam apicalem ferentibus. Nomen e *nephele* (Gr.): species generis in silvis nubilis plerumque habitantes. Typus: *Nephelea polystichoides* (Christ) Tryon (*Alsophila polystichoides* Christ), Costaricae.

Petiole with squaminate spines, these large, black, mostly obturbinate, with a slender apex, the unexpanded croziers with well developed squaminate spines, many of them caducous, lacking trichomes; petiole *scales* patent, fully adnate or slightly narrowed at the base, structurally marginate, with a narrow to broad margin of cells different in orientation, size, shape, and usually in color from those of the central portion, bearing a dark seta at the apex and sometimes one or more on the edge or body of the scale; *minute indument* of the petiole, when present, of trichomidia and (or) of squamulae; *costa* pubescent above; *veins* free, in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* present, hemitelioid to sphaeropteroid.

Nephelea (Figs. 3, 31–38) is an American genus of about 30 species. It is especially distinctive in its squaminate spines that are present on the petiole and are precociously developed on the croziers. Typical petiole spines and the spiny crozier are illustrated in Fig. 31. There is evidence clearly indicating that these spines have evolved from petiole scales. Species of *Nephelea* have some petiole scales thickened basally, some that are spine-like, and some that are small spines with the differentiated margins of the normal scales on each side (Figs. 32–34), as well as the larger spines. These transitional stages are indicative of a squamate origin of the spine proper, as are the caducous spines of the croziers that become detached at their very base. As noted in the discussion under *Alsophila*, the series of species leading to *A. auriculata* illustrates how, in *Nephelea*, the spines may also have evolved by thickening the sclerotic central portion of the scale.

The lamina bears scales similar to those of the petiole, but much smaller, and these are an aid in identifying specimens of *Nephelea* that lack the petiole. However, similar small laminar scales with dark setae also occur on some American species of *Alsophila*. Some characters which show interesting evolutionary developments are not mentioned in the description because they do not occur in all or most of the species. These are the pubescent indusium of species such as *N. portoricensis* and *N. cuspidata*, the spiny stems of species such as *N. polystichoides* and *N. aureonitens* (Fig. 38) and the very small petiole scales of species such as *N. Sternbergii*. The chromosome number of $n=69$ has been reported by Walker (1966) for *N. Tussacii* and *N. Grevilleana* (as *Cyathea Tussacii* and *C. Grevilleana*, respectively).

The following list of species will serve as examples of the genus. It does not include those in which problems of taxonomy or nomenclature are known.

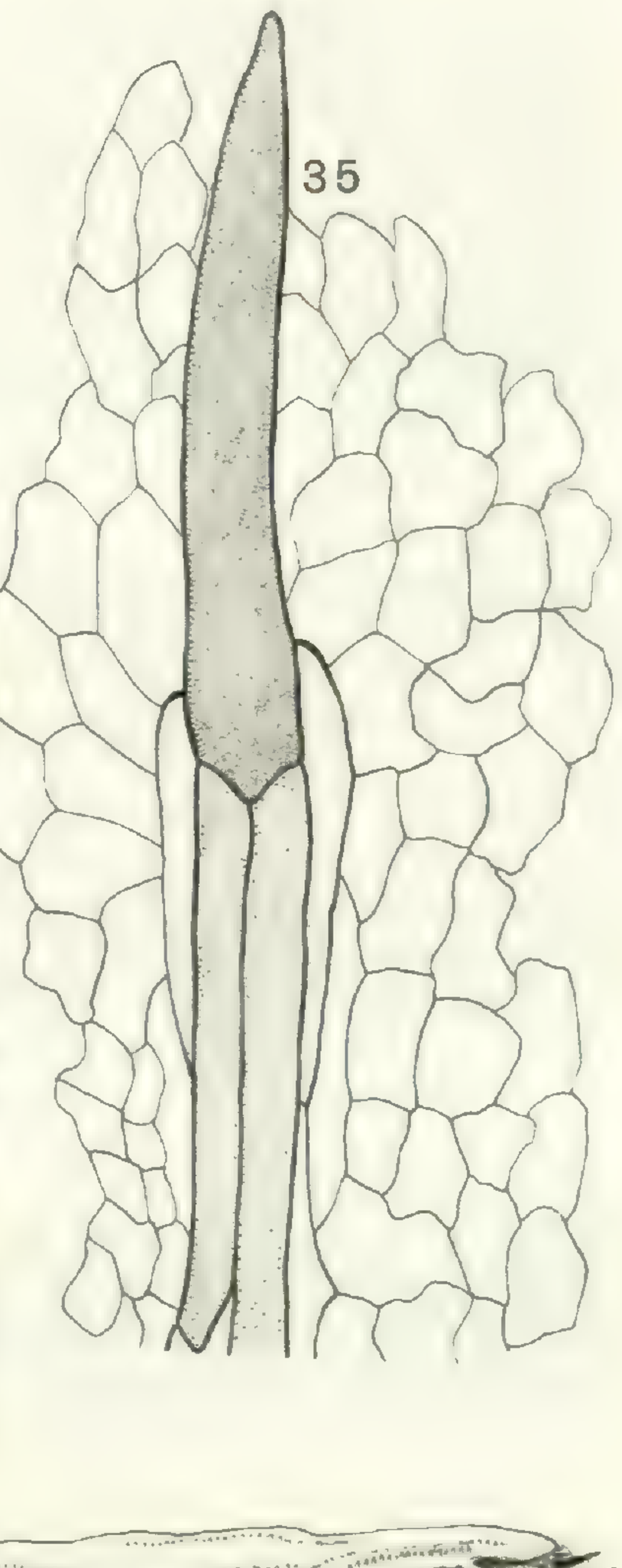
WEST INDIES

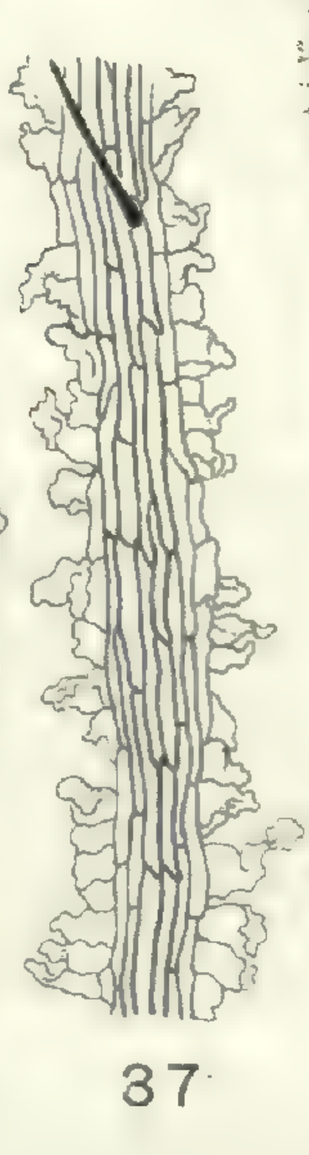
Nephelea araneosa (Maxon) Tryon, comb. nov., *Cyathea araneosa* Maxon, North Amer. Fl. **16**:74. 1909.

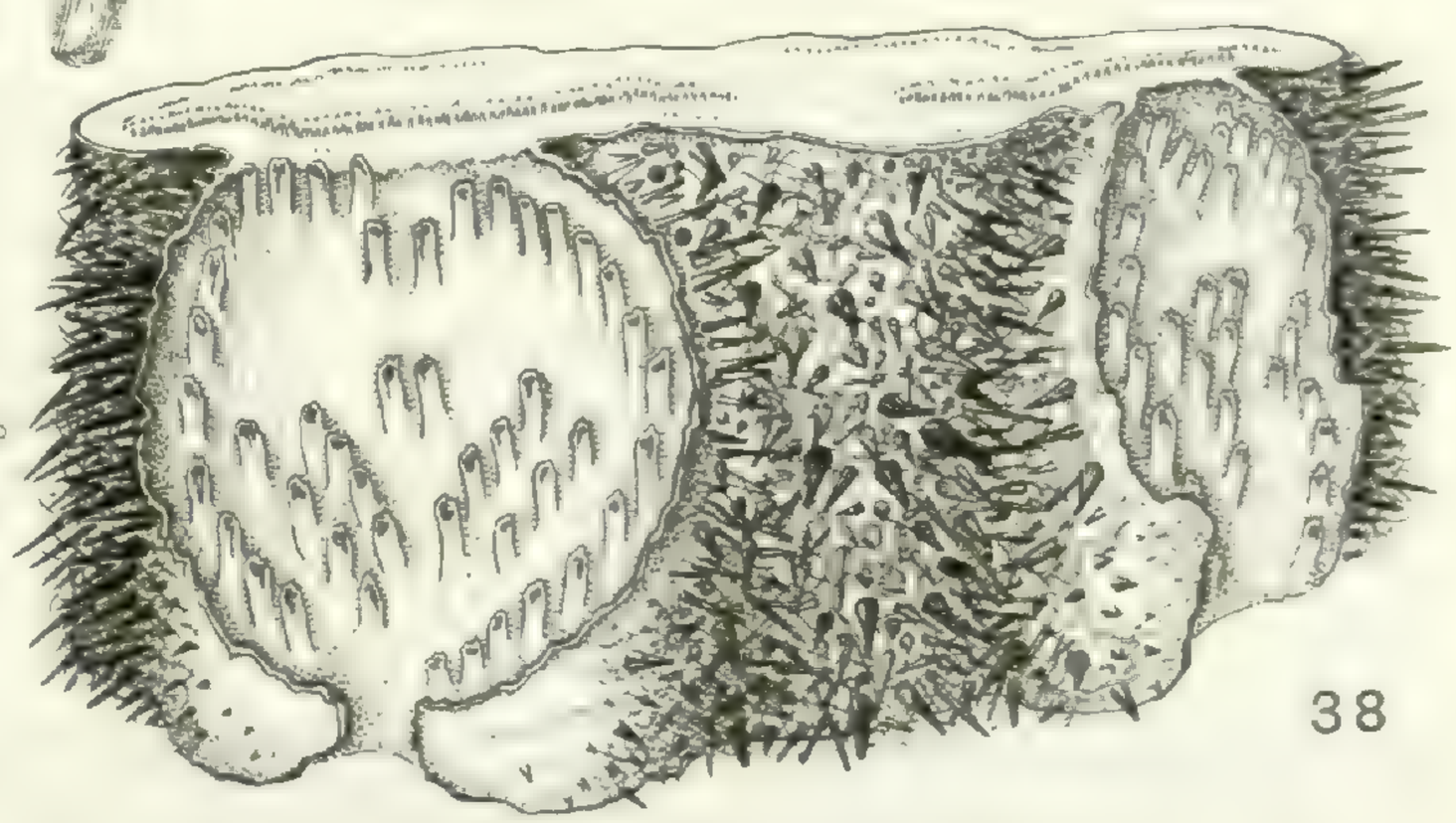
N. balanocarpa (D. C. Eaton) Tryon, comb. nov., *Cyathea balanocarpa* D. C. Eaton, Mem. Amer. Acad. n.s. 8:215. 1860.

N. concinna (Baker) Tryon, comb. nov., *Cyathea arborea* var. *concinna* Baker, Jour. Bot. **19**:52. 1881, *Cyathea concinna* (Baker) Jenm.

N. crassa (Maxon) Tryon, comb. nov., *Cyathea crassa* Maxon, Contrib. U. S. Nat. Herb. **13**:40. 1909.







FIGS. 31–38. NEPHELEA. FIG. 31. Unexpanded crozier of *N. polystichoides, Gastony 793,* × 1, GH, the apical portion is the unexpanded crozier proper with spines among the scales, the basal portion has been detached from the stem and shows spines typical of the stem and petiole base. FIGS. 32–34. Transitions from petiole scales to squaminate spines, *N. aureonitens, Gastony 763,* all × 8, GH. 32, Petiole scale thickened basally. 33, Spine-like petiole scale. 34, Small squaminate spine. FIGS. 35–37. Portions of petiole scales: 35, Apex, *N. purpurascens, Sodiro,* July 1907, × 150, US. 36, Apex, *N. Sternbergii, Mexia 4650,* × 30, GH. 37, *N. Sternbergii, Dusén 6775,* × 30, GH. FIG. 38. Portion of spiny stem of *N. aureonitens, Gastony 763,* × 1, GH.

N. cubensis (Maxon) Tryon, comb. nov., *Cyathea cubensis* Maxon, North Amer. Fl. **16**:73. 1909.

N. Grevilleana (Mart.) Tryon, comb. nov., *Cyathea Grevilleana* Mart. Icon. Pl. Crypt. Bras. 78. 1834.

N. Hieronymi (Brause) Tryon, comb. nov., *Cyathea Hiermonymi* Brause, in Urban, Symb. Ant. **7**:152. 1911.

N. Imrayana (Hook.) Tryon, comb. nov., *Cyathea Imrayana* Hook. Sp. Fil. **1**:18. 1844.

N. portoricensis (Kuhn) Tryon, comb. nov., *Cyathea portoricensis* Kuhn, Linnaea **36**:163. 1869.

N. pubescens (Kuhn) Tryon, comb. nov., *Cyathea pubescens* Kuhn, Linnaea **36**:164. 1869.

N. Tussacii (Desv.) Tryon, comb. nov., *Cyathea Tussacii* Desv. Mém. Soc. Linn. Paris **6**:323. 1827.

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Nephelea aureonitens (Christ) Tryon, comb. nov., *Cyathea aureonitens* Christ, Bull. Herb. Boiss. II, **4**:948. 1904.

N. basilaris (Christ) Tryon, comb. nov., *Cyathea basilaris* Christ, Bull. Herb. Boiss. II, **4**:949. 1904.

N. mexicana (Schlect. & Cham.) Tryon, comb. nov., *Cyathea mexicana* Schlect. & Cham. Linnaea **5**:616. 1830.

N. patellaris (Christ) Tryon, comb. nov., *Cyathea patellaris* Christ, Ann. Conserv. Jard. Bot. Genève **4**:207. 1900.

N. polystichoides (Christ) Tryon, comb. nov., *Alsophila polystichoides* Christ, Bull. Soc. Bot. Belg. **35** (Mém.): 177. 1896.

N. tenerifrons (Christ) Tryon, comb. nov., *Alsophila tenerifrons* Christ, Bull. Herb. Boiss. **II**, **4**:959. 1904.

[*Cyathea Werckleana*=**Nephelea polystichoides**].

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Nephelea canescens (Sod.) Tryon, comb. nov., *Cyathea canescens* Sod. Sert. Fl. Ecuad. **2**:4. 1908.

N. cuspidata (Kze.) Tryon, comb. nov., *Cyathea cuspidata* Kze. Linnaea **9**:101. 1834.

N. erinacea (Karst.) Tryon, comb. nov., *Cyathea erinacea* Karst. Linnaea **28**:453. 1857.

N. purpurascens (Sod.) Tryon, comb. nov., *Cyathea purpurascens* Sod. Crypt. Vasc. Quit. 503. 1893.

N. setosa (Kaulf.) Tryon, comb. nov., *Alsophila setosa* Kaulf. Enum. Fil. 249. 1824, *Hemitelia setosa* (Kaulf.) Mett.

N. Sternbergii (Sternb.) Tryon, comb. nov., *Cyathea Sternbergii* Sternb. Fl. von Vorwelt **1**:47. 1820 (I have seen only Fl. Monde Primitif **4**:52. 1826).

6. Trichipteris

Trichipteris Presl, Delic. Prag. **1**:172. 1822, often as *Trichopteris*. Type: *Trichipteris excelsa* Presl = *Trichipteris corcovadensis* (Raddi) Copel.

Chnoophora Kaulf. Enum. Fil. 250. 1824. Type: *Chnoophora Humboldtii* Kaulf., nom. superfl. for *Cyathea villosa* Willd. = *Trichipteris villosa* (Willd.) Tryon.

Petiole smooth to tuberculate, or with corticinate spines, often with trichomes; petiole *scales* (especially on the abaxial side) more or less appressed, attached at one point of a pseudopeltate or peltate base, structurally marginate, with a narrow to broad margin of cells different in orientation, size, and usually in shape and color from those of the central portion, lacking dark setae, the apex rounded to filamentous; *minute indument* of the petiole, when present, rarely of patent trichomidia, usually of squamulae; *costa* usually pubescent above, rarely glabrous; *veins* free (rarely some branch and rejoin), in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* absent.

The alteration of the spelling of *Trichipteris* to *Trichopteris*, initiated by Schott (Gen. Fil. 1834) and later accepted by Presl and other authors, cannot be maintained. *Trichipteris* was used for the genus, for the species and in the index of the original publication. Although the name was derived from "trichos" and "pteros," and *Trichopteris* may be considered as preferable, Presl's original choice in the formation of the compound must stand.

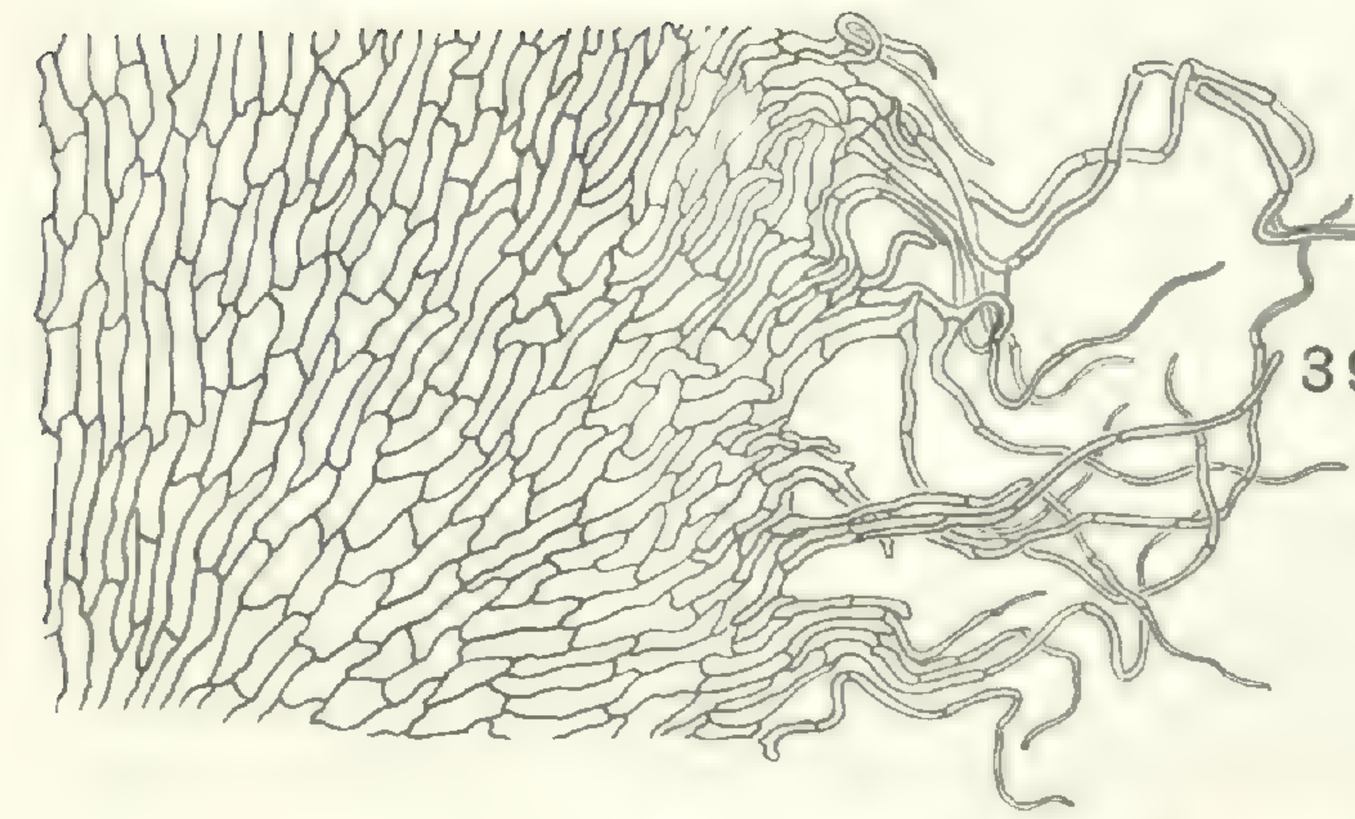
Martius is frequently credited with the valid publication of a genus *Chnoophora*, in his Icones Pl. Crypt. Brasil. 1834, but this is evidently incorrect. In the formal taxonomic treatment, pages 62–63, Martius explicitly treats *Chnoophora* Kaulf. as a synonym of *Alsophila* and as a section or subgenus of it. The species that appears as *C. excelsa* on t. 27 and t. 37 is given in the text as *Alsophila (Chnoophora) excelsa*. I believe that the formal text must take precedence in this case, and in others where the name *Chnoophora* is used. The generic name, when used by itself, should be ascribed to Kaulfuss and new binomials with it treated as published in synonymy.

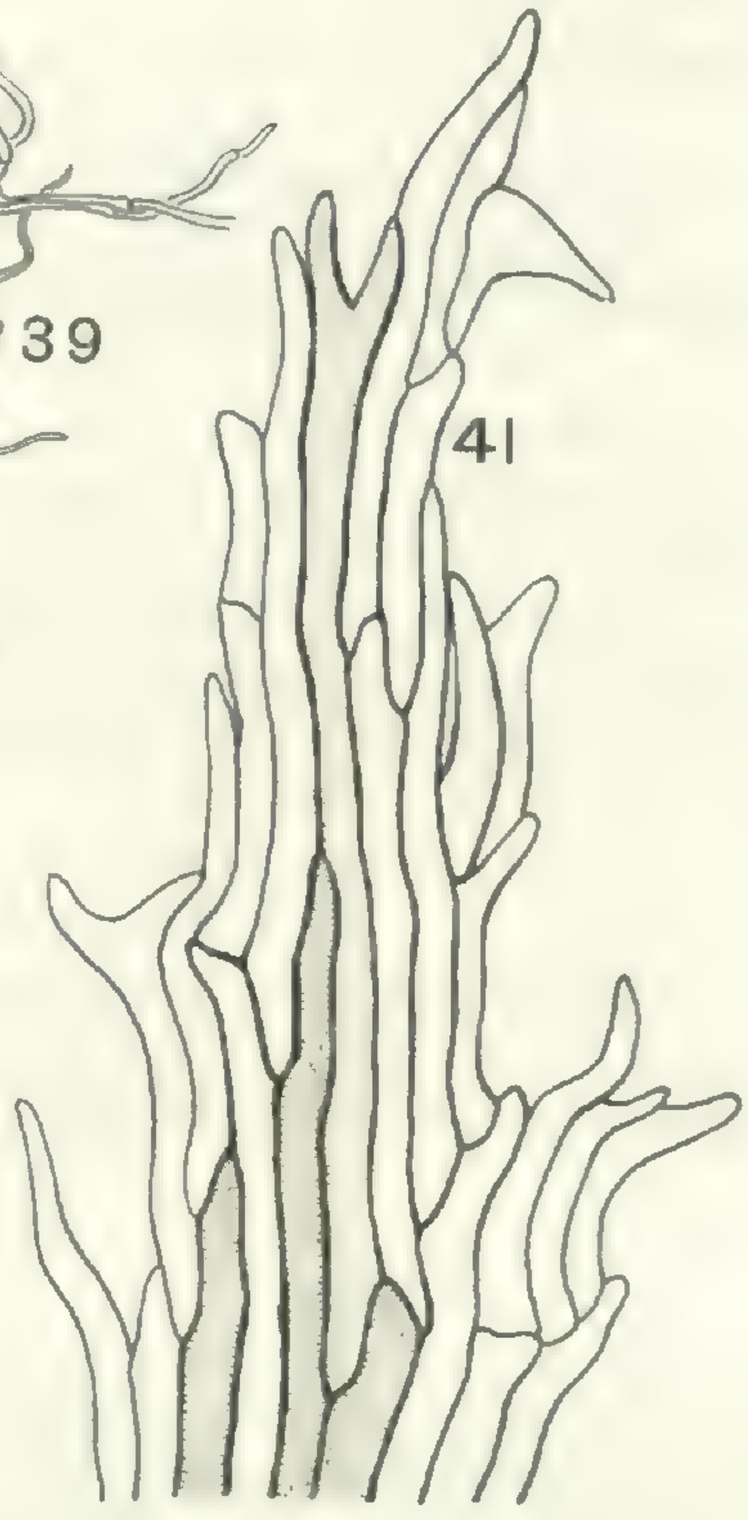
Trichipteris (Figs. 39–43) is an American genus of about 90 species. It is characterized by marginate petiole scales that lack dark setae, normal, free venation (Figs. 42–43) and absence of an indusium. *Trichipteris* is nearly the equivalent of the classical *Alsophila*, in America, because there are only a few exindusiate species belonging to other genera in the neotropics. The cellular differentiation of the petiole scales is usually similar to that in *Cyathea* and is described in some detail there. In some species, such as *T. albidopaleata* and *T. aspera*, the modified margin is very narrow; in others such as *T. scabriuscula* it is rather broad but poorly developed; in *T. Wendlandii*, although definite, it is both narrow and slightly modified. These examples of species with only slightly marginate scales nearly provide a connection with

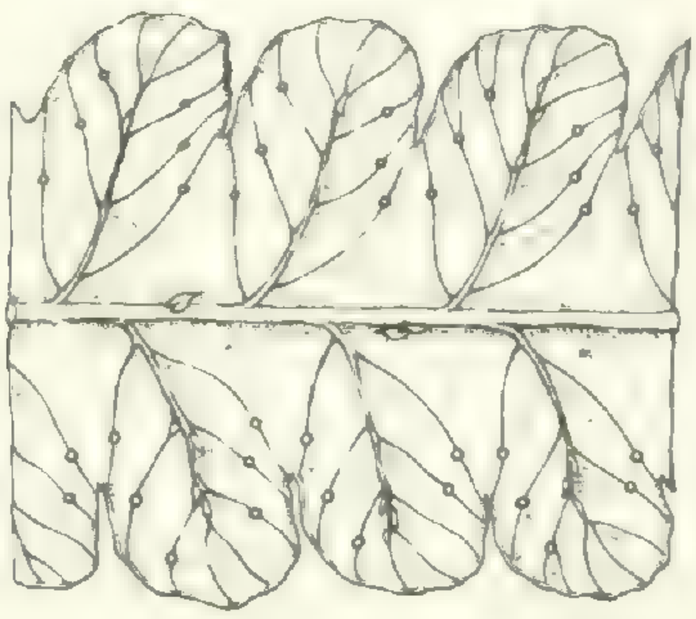
Sphaeropteris in which some species have tendencies toward marginate scales. Species of *Trichipteris* often grow at lower altitudes than those of other genera and it the only genus represented in the Amazon basin. The chromosome number of $n=69$ has been reported by Walker (1966) for *T. armata* (as *Cyathea armata*).

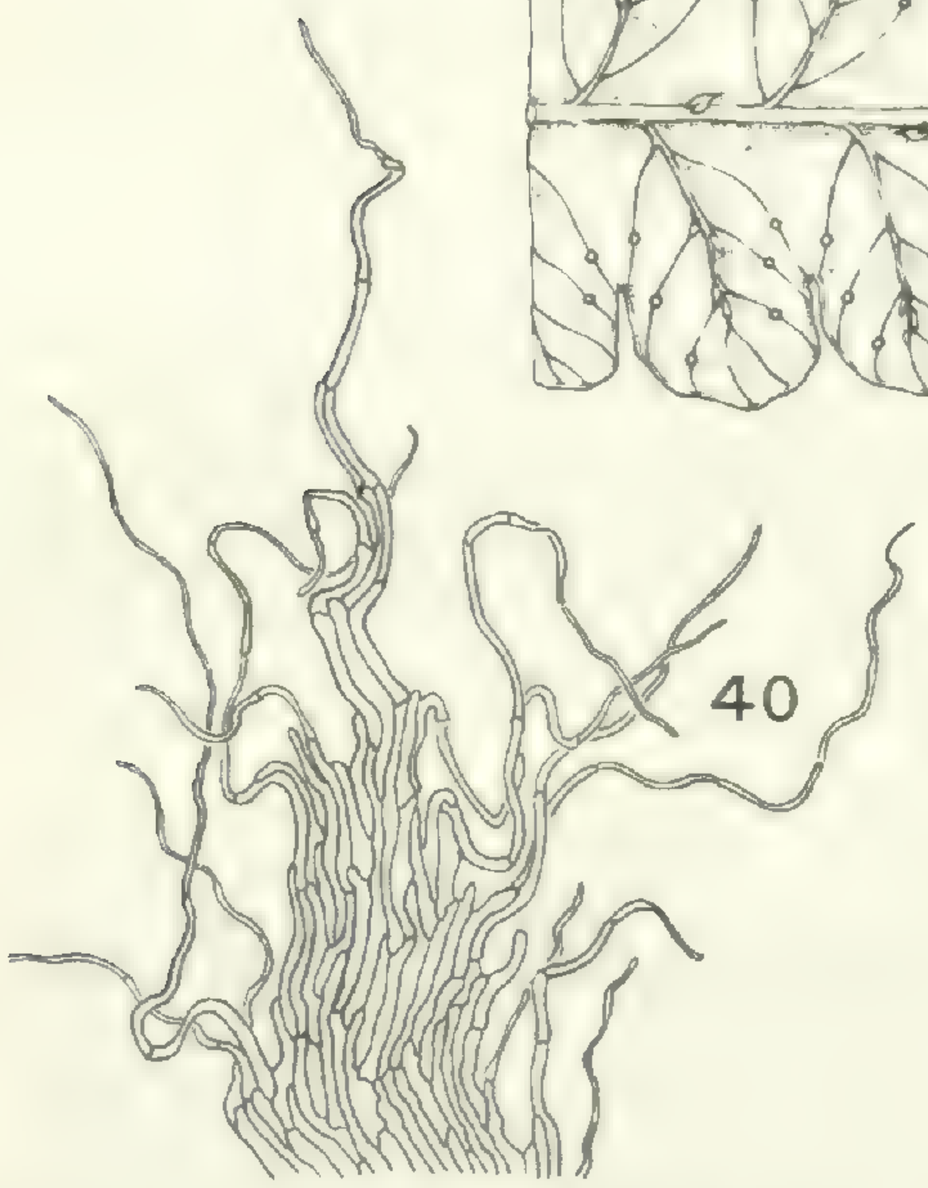
Recognition of *Trichipteris* and *Cyathea* as genera is based on evidence that each represents a separate evolutionary line. They are undoubtedly closely related and their evolutionary status and affinities could also be expressed by their classification as subgenera. However, the large numbers of species in each enforces their claim to generic rank. A comparison of the species in these two genera has shown very few cases of close similarity between indusiate species of *Cyathea* and exindusiate *Trichipteris*. Aside from these cases, species groups and distinctive species seem to have closest affinities within their own genus.

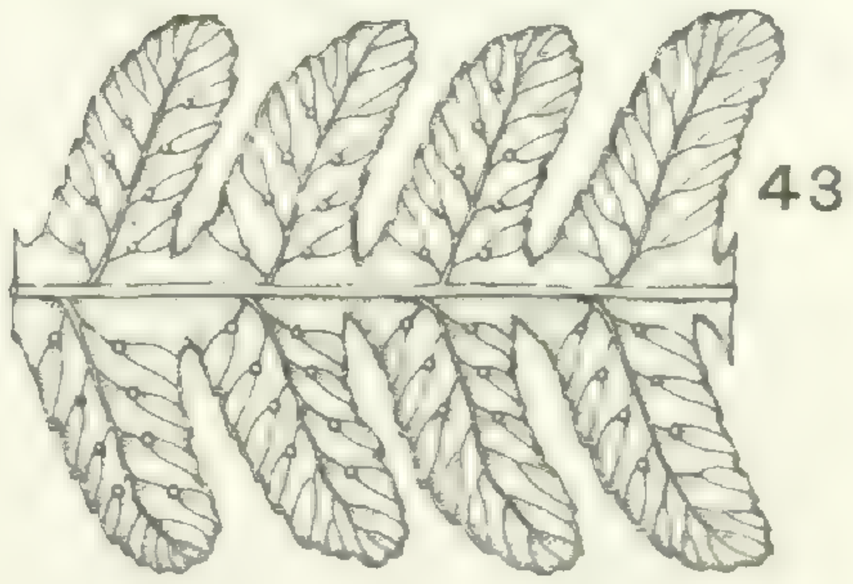
There are three groups of species that might indicate an intimate relation between *Trichipteris* and *Cyathea:* (1) *Trichipteris armata* and *T. bicrenata* with *Cyathea acutidens* and *C. leucolepis-mata;* (2) *Trichipteris obtusa, T. oblonga* and *T. chnoodes* with *Cyathea columbiana;* and (3) *Trichipteris pubescens* and an undescribed allied species with two undescribed species of *Cyathea*. Similarities among the species in these three groups are in characters of the lamina architecture and indument, the venation, the relative length of the petiole and lamina and the habit. These characters may show convergent evolution in species of different genera. This interpretation is especially clear in the species of the third group. These four species all have a short petiole and a pinnate-pinnatifid lamina of similar size and shape which is pubescent on both surfaces. However, the two exindusiate species of *Trichipteris* have similar paraphyses and petiole scales and in these structures they differ from the two similar indusiate species of *Cyathea*. The characters common to the two pairs of species are best interpreted as convergent. Characters of the paraphyses and the details of the petiole scales, in addition to the indusium, are alike in members of other species-groups and they are a more certain guide to evolutionary affinity than the size, architecture and shape of the lamina and its pubescence.











FIGS. 39–43. TRICHIPTERIS. FIGS. 39–41. Portions of petiole scales: 39, *T. mexicana, Yuncker et al. 6015,* × 30, GH. 40, Apex, *T. mexicana* (as in Fig. 39). 41, Apex, *T. albidopaleata, Mexia 4869,* × 150, GH. FIGS. 42–43. Portions of pinnules showing venation and receptacles, all × 2. 42, *T. arbuscula, Brade 8255,* US. 43, *T. compta, L. B. Smith 6579,* US.

The following list of species will serve as examples of the genus. It does not include those in which problems of taxonomy or nomenclature are known.

WEST INDIES

Trichipteris armata (Sw.) Tryon, comb. nov., *Polypodium armatum* Sw. Prod. Veg. Ind. Occ. 134. 1788, *Alsophila armata* (Sw.) Presl, not Mart., *Alsophila Swartziana* Mart.

T. aspera (L.) Tryon, comb. nov., *Polypodium asperum* L. Sp. Pl. **2**:1093. 1753, *Alsophila aspera* (L.) Spreng.

T. borinquena (Maxon) Tryon, comb. nov., *Alsophila borinquena* Maxon, Amer. Fern Jour. **15**:56. 1925.

T. Eatonii (Jenm.) Tryon, comb. nov., *Alsophila Eatonii* Jenm. Journ. Bot. **25**:98. 1887.

T. Estellae (Riba) Tryon, comb. nov., *Alsophila Estellae* Riba, Rhodora **69**:67. 1967.

T. Hodgeana (Proctor) Tryon, comb. nov., *Cyathea Hodgeana* Proctor, Rhodora **63**:31. 1961.

T. sagittifolia (Hook.) Tryon. comb. nov., *Alsophila sagittifolia* Hook. Syn. Fil. 37. 1866.

T. strigillosa (Maxon) Tryon, comb. nov., *Alsophila strigillosa* Maxon, Contrib. U. S. Nat. Herb. **24**:37. 1922.

[*Alsophila Swartziana*=**Trichipteris armata**].

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Trichipteris bicrenata (Liebm.) Tryon, comb. nov., *Cyathea bicrenata* Liebm. Vid. Selsk. Skr. V, 1:289. 1849, *Alsophila bicrenata* (Liebm.) Fourn.

T. chnoodes (Christ) Tryon, comb. nov., *Alsophila chnoodes* Christ, Bull. Herb. Boiss. II, **4**:958. 1904.

T. mexicana (Mart.) Tryon, comb nov., *Alsophila mexicana* Mart. Icon. Pl. Crypt. Bras. 70. 1834.

T. nesiotica (Maxon) Tryon, comb. nov., *Alsophila nesiotica* Maxon, Contrib. U. S. Nat. Herb. **24**:43. 1922, (Cocos Is.).

T. pansamalana (Maxon) Tryon, comb. nov., *Alsophila pansamalana* Maxon, Contrib. U. S. Nat. Herb. **24**:40. 1922.

T. scabriuscula (Maxon) Tryon, comb. nov., *Alsophila scabriuscula* Maxon, Proc. Biol. Soc. Wash. **32**:125. 1919.

T. Schiediana (Presl) Tryon, comb. nov., *Alsophila Schiediana* Presl, Tent. Pterid. 62. 1836.

T. stipularis (Christ) Tryon, comb. nov., *Alsophila stipularis* Christ, Bull. Herb. Boiss. II, **4**:958. 1904.

T. trichiata (Maxon) Tryon, comb. nov., *Alsophila trichiata* Maxon, Contrib. U. S. Nat. Herb. **24**:44. 1922.

T. ursina (Maxon) Tryon, comb. nov., *Alsophila ursina* Maxon, Jour. Wash. Acad. Sci. **34**:48. 1944.

T. Wendlandii (Kuhn) Tryon, comb. nov., *Alsophila Wendlandii* Kuhn, Linnaea **36**:158. 1869.

T. Williamsii (Maxon) Tryon, comb. nov., *Alsophila Williamsii* Maxon, Contrib. U. S. Nat. Herb. **24**:46. 1922.

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Trichipteris albidopaleata (Copel.) Tryon, comb. nov., *Cyathea albidopaleata* Copel. Univ. Calif. Publ. Bot. **17**:25. 1932, *Alsophila albidopaleata* (Copel.) C.Chr.

T. anacampta (Alston) Tryon, comb. nov., *Cyathea anacampta* Alston, Jour. Wash. Acad. Sci. **48**:230. 1958.

T. arbuscula (Kze.) Tryon, comb. nov., *Alsophila arbuscula* Kze. Bot. Zeit. **2**:313. 1844.

T. atrovirens (Langsd. & Fisch.) Tryon, comb. nov., *Polypodium atrovirens* Langsd. & Fisch. Icon. Fil. 12. 1810, *Alsophila atrovirens* (Langsd. & Fisch.) Presl.

T. bulligera (Rosenst.) Tryon, comb. nov., *Alsophila bulligera* Rosenst. Fedde Repert. **25**:57. 1928.

T. caracasana (Kl.) Tryon, comb. nov., *Alsophila caracasana* Kl. Linnaea **18**:541. 1844.

T. compta (Mart.) Tryon, comb. nov., *Alsophila compta* Mart. Icon. Pl. Crypt. Bras. 66. 1834.

T. conjugata (Hook.) Tryon, comb. nov., *Alsophila conjugata* Hook. Syn. Fil. 37. 1866.

T. corcovadensis (Raddi) Copel., *Alsophila corcovadensis* (Raddi) C.Chr.

T. cordata (Kl.) Tryon, comb. nov., *Alsophila cordata* Kl. Linnaea **20**:441. 1847.

T. crassa (Karst.) Tryon, comb. nov., *Alsophila crassa* Karst. Fl. Columb. **2**:187. 1869.

T. decomposita (Karst.) Tryon, comb. nov., *Alsophila decomposita* Karst. Fl. Columb. **2**:185. 1869.

T. demissa (Morton) Tryon, comb. nov., *Alsophila demissa* Morton, Fieldiana Bot. **28**:7. 1951.

T. dicromatolepis (Fée) Tryon, comb. nov., *Alsophila dicromatolepis* Fée, Crypt. Vasc. Brésil **1**:164. 1869.

T. elegans (Mart.) Presl, *Alsophila elegans* Mart.

T. floribunda (Baker) Tryon, comb. nov., *Alsophila floribunda* Baker, Syn. Fil. ed 2, 458. 1874.

T. frigida (Karst.) Tryon, comb. nov., *Alsophila frigida* Karst. Fl. Columb. **1**:61. 1860.

T. Gardneri (Hook.) Tryon, comb. nov., *Alsophila Gardneri* Hook. Sp. Fil. **1**:40. 1844.

T. Glaziovii (Fée) Tryon, comb. nov., *Alsophila Glaziovii* Fée, Crypt. Vasc. Brésil **1**:160. 1869.

T. Gleasonii (Maxon) Tryon, comb. nov., *Alsophila Gleasonii* Maxon, Amer. Fern Jour. **15**:55. 1925.

T. hirsuta (Presl) Tryon, comb. nov., *Cyathea hirsuta* Presl, Delic. Prag. 190. 1822. *Alsophila hirsuta* (Presl) Kze.

T. infesta (Kze.) Tryon, comb. nov., *Alsophila infesta* Kze. Linnaea **9**:98. 1834.

T. Kalbreyeri (C.Chr.) Tryon, comb. nov., *Alsophila Kalbreyeri* C.Chr. Ind. Fil. 44. 1905 (nom. nov. for *Alsophila podophylla* Baker, not Hook.).

T. Kuhnii (Hieron.) Tryon, comb. nov., *Nephrodium Kuhnii* Hieron. Engl. Bot. Jahrb. **34**:440. 1904, *Alsophila Kuhnii* (Hieron.) C.Chr.

T. lasiosora (Kuhn) Tryon, comb. nov., *Alsophila lasiosora* Kuhn, Linnaea **36**:157. 1869.

T. latevagans (Baker) Tryon, comb. nov., *Alsophila latevagans* Baker, Jour Bot. **19**:203. 1881.

T. Lechleri (Mett.) Tryon, comb. nov., *Alsophila Lechleri* Mett. Fil. Lechl. **2**:28. 1859.

T. leucolepis (Mart.) Tryon, comb. nov., *Alsophila leucolepis* Mart. Icon. Pl. Crypt. Bras. 70. 1834.

T. Mellobarretoi (Brade) Tryon, comb. nov., *Alsophila Mello-barretoi* Brade, Arq. Jard. Bot. Rio Janeiro **11**:22. 1951.

T. Mexiae (Copel.) Tryon, comb. nov., *Cyathea Mexiae* Copel. Univ. Calif. Publ. Bot. **17**:30. 1932.

T. microdonta (Desv.) Tryon, comb. nov., *Polypodium microdontum* Desv. Ges. Naturf. Freunde Berl. Mag. **5**:319. 1811, *Alsophila microdonta* (Desv.) Desv.

T. microphylla (Kl.) Tryon, comb. nov., *Alsophila microphylla* Kl. Linnaea **18**:541. 1844.

T. Miersii (Hook.) Tryon, comb. nov., *Alsophila Miersii* Hook. Sp. Fil. **1**:38. 1844.

T. nigra (Mart.) Tryon, comb. nov., *Alsophila nigra* Mart. Icon. Pl. Crypt. Bras. 71. 1834.

T. oblonga (Kl.) Tryon, comb. nov., *Alsophila oblonga* Kl. Linnaea **18**:540. 1844.

T. obtusa (Kl.) Tryon, comb. nov., *Alsophila obtusa* Kl. Allgm. Gartenzeit. **30**:41. 1852.

T. pastazensis (Hieron.) Tryon, comb. nov., *Alsophila pastazensis* Hieron. Hedwigia **45**:232. 1906.

T. pauciflora (Presl) Tryon, comb. nov., *Alsophila pauciflora* Presl, Gefässbündel Stipes der Farrn 35. 1847 (preprint from Abhandl. böhm. Ges. V, **5**:343. 1848), (sp. nov. based on taxon sub nom. *Alsophila aculeata* (Kaulf.) Kl. Linnaea **18**:540. 1844).

T. phalaenolepis (C.Chr.) Tryon, comb. nov., *Alsophila phalaenolepis* C.Chr. Fedde Repert. **10**:213. 1911.

T. phegopteroides (Hook.) Tryon, comb. nov., *Alsophila phegopteroides* Hook. Syn. Fil. 32. 1865.

T. Portoana (Brade) Tryon, comb. nov., *Alsophila Portoana* Brade, Arch. Instit. Biol. Veg. Rio Janeiro **1**:223. 1935.

T. praecincta (Kze.) Tryon, comb. nov., *Alsophila praecincta* Kze. Flora 1839 (1): Beibl. 53.

T. procera (Willd.) Tryon, comb. nov., *Polypodium procerum* Willd. Sp. Pl. **5**:206. 1810.

T. pubescens (Baker) Tryon, comb. nov., *Alsophila pubescens* Baker, Syn. Fil. 449. 1868.

T. pungens (Willd.) Tryon, comb. nov., *Polypodium pungens* Willd. Sp. Pl. **5**:206. 1810, *Alsophila pungens* (Willd.) Presl.

T. rufa (Fée) Tryon, comb. nov., *Alsophila rufa* Fée, Crypt. Vasc. Brésil **1**:166. 1869.

T. submarginalis (Domin) Tryon, comb. nov., *Alsophila submarginalis* Domin, Kew Bull. 1929: 217.

T. Tryonorum (Riba) Tryon, comb. nov., *Alsophila Tryonorum* Riba, Rhodora **69**:66. 1967.

T. Ulei (Christ) Tryon, comb. nov., *Alsophila Ulei* Christ, Hedwigia **44**:367. 1905.

T. vernicosa (Kuhn) Tryon, comb. nov., *Alsophila vernicosa* Kuhn, Linnaea **36**:155. 1869.

T. villosa (Willd.) Tryon, comb. nov., *Cyathea villosa* Willd. Sp. Pl. **5**:495. 1810, *Alsophila villosa* (Willd). Desv.

7. Cyathea

Cyathea Sm. Mém. Acad. Turin, **5**:416. 1793. Type: *Cyathea arborea* (L.) Sm. (*Polypodium arboreum* L.).

Hemitelia R. Br. Prod. Fl. Nov. Holl. 158. 1810. Type: *Cyathea multiflora* Sm. (Brown did not make any combinations for the names of the species of his new genus).

Disphenia Presl, Tent. Pterid. 55. 1836, nom. superfl. Type: the same as that of *Cyathea* (all species, except *Cyathea arborea,* that were originally included in *Cyathea* had, prior to Presl's publication, been removed to other genera: two species of the original six to *Cystopteris* and three species to *Hemitelia*).

Cormophyllum Newm. Phytol. 5:237. 1856, nom. superfl. Type: the same as that of *Cyathea* (Newman included *Polypodium arboreum* L. in his genus).

Petiole smooth to tuberculate, or with corticinate spines, sometimes with trichomes; petiole *scales* (especially on the abaxial side) more or less appressed, attached at one point of a pseudopeltate or peltate base, structurally marginate, with a narrow to broad margin of cells different in orientation, size and usually in shape and color from those of the central portion, lacking dark setae, the apex rounded to filamentous; *minute indument* of the petiole, when present, of squamulae and (or) rarely of patent trichomidia; *costa* pubescent above; *veins* free, in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* present, scale-like to sphaeropteroid.

Cyathea (Figs. 4, 10, 44–46) is an American genus of about 110 species. It is characterized by marginate petiole scales that lack a dark seta, normal, free venation (as in Figs. 42–43) and the presence of an indusium. The separation of exindusiate *Trichipteris* and indusiate *Cyathea* has been discussed under the former genus. The petiole scales of *Trichipteris, Cyathea* and *Cnemidaria* are similar in having a cellular differentiation of the margin (Figs. 39, 44–46). The central portion is of large, elongate cells with their long axis parallel to that of the scale; beyond this center the cells become progressively smaller, often more rectangular, and finally oriented approximately at a right angle to the edge of the scale. There is also usually (but not always) a transition from heavy walled and dark colored central cells to thin walled and light colored marginal cells which often gives the scale a bi-colorous appearance. Species of *Cyathea* with a sphaeropteroid indusium are especially numerous in the northern Andes where they seem to form a large group of closely related species. The chromosome number of $n=69$ has been reported by Walker (1966) for *Cyathea arborea*.

The following list of species will serve as examples of the genus. It does not include those in which problems of taxonomy or

nomenclature are known. It includes only a selection of the many closely related and inadequately known species of the northern Andean region, especially of Ecuador and Colombia.

WEST INDIES

Cyathea aquilina (Christ) Domin, *Alsophila aquilina* Christ.
C. arborea (L.) Sm.
C. asperula Maxon.
C. Brittoniana Maxon.
C. calolepis (Hook.) Domin, *Hemitelia calolepis* Hook.
C. dissoluta Jenm.
C. furfuracea Baker.
C. gracilis Griseb.
C. Harrisii Maxon.
C. Lewisii (Morton & Proctor) Proctor, *Hemitelia Lewisii* Morton & Proctor.
C. muricata Willd., *Hemitelia muricata* (Willd.) Fée.
C. parvula (Jenm.) Domin, *Alsophila parvula* Jenm.
C. producta Maxon.
C. Sherringii (Jenm.) Domin, *Hemitelia Sherringii* Jenm.
C. tenera Griseb.

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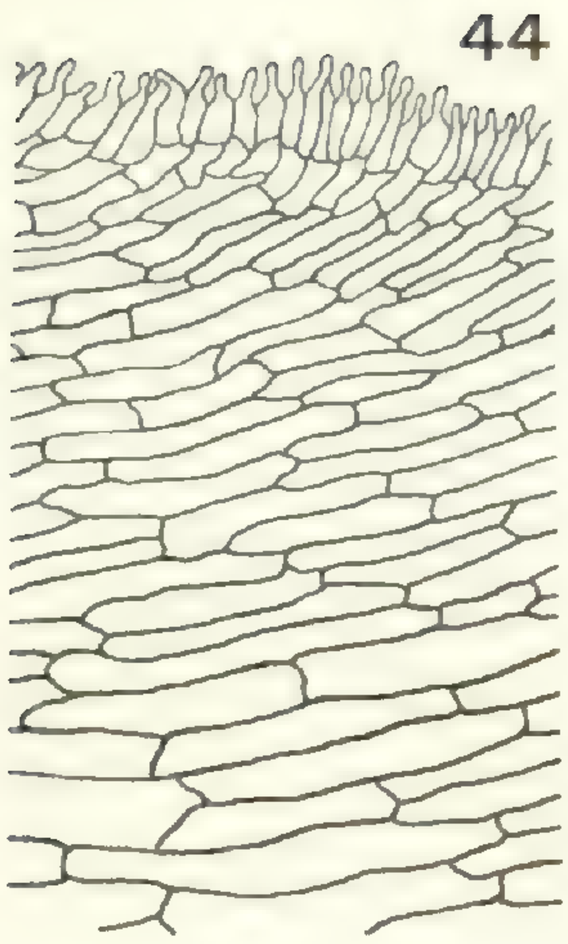
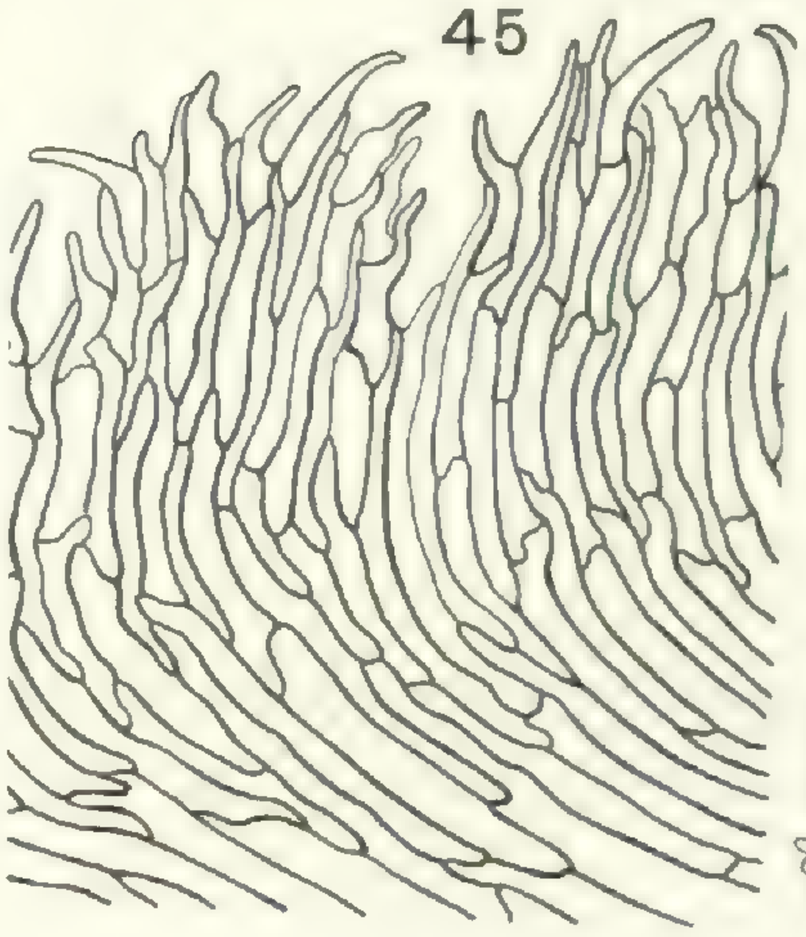
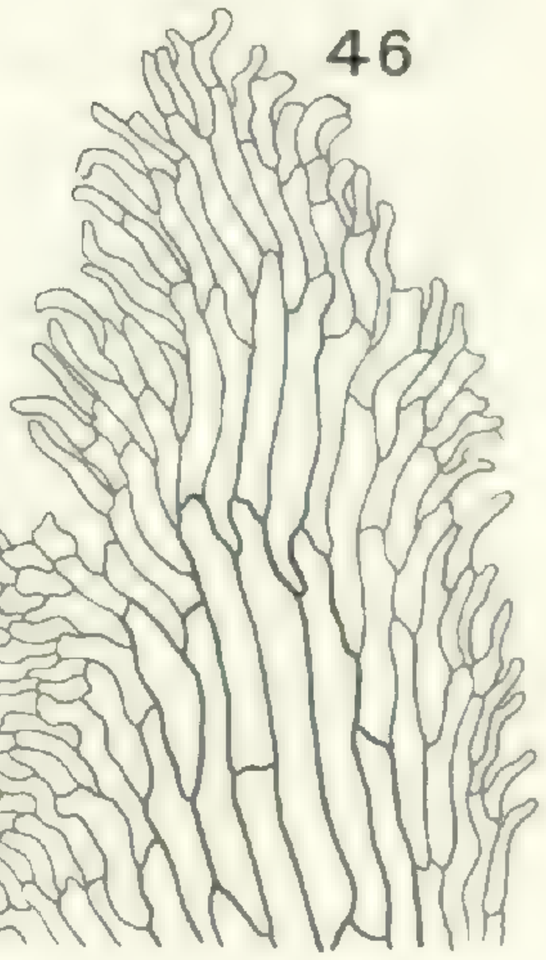
Cyathea acutidens (Christ) Domin, *Alsophila acutidens* Christ.
C. aphlebioides Christ.
C. conspersa Christ.
C. costaricensis (Kuhn) Domin, *Hemitelia costaricensis* Kuhn.
C. delicatula Maxon.
C. fulva (Mart. & Gal.) Fée, *Alsophila fulva* Mart. & Gal.
C. Jurgensenii Fourn.
C. Maxonii Maxon.
C. multiflora Sm., *Hemitelia multiflora* (Sm.) Spreng.
C. notabilis Domin, *Alsophila notabilis* Maxon, 1922, not Saporta, Mém. Soc. Géol. France II, 8:329. 1868. (Cocos Is.).
C. onusta Christ.
C. pelliculosa Christ.
C. suprastrigosa (Christ) Maxon, *Hemitelia suprastrigosa* Christ.
C. Tuerckheimii Maxon.

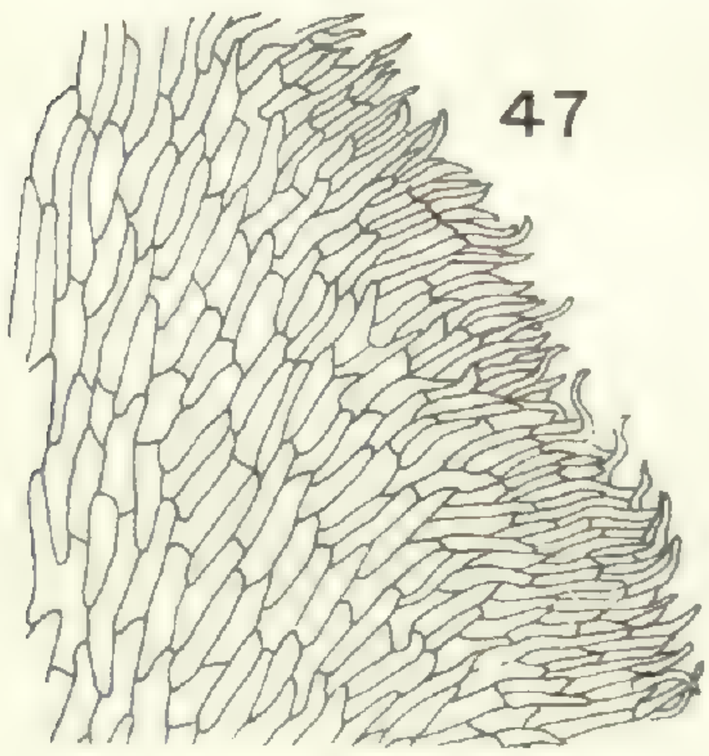
SOUTH AMERICA

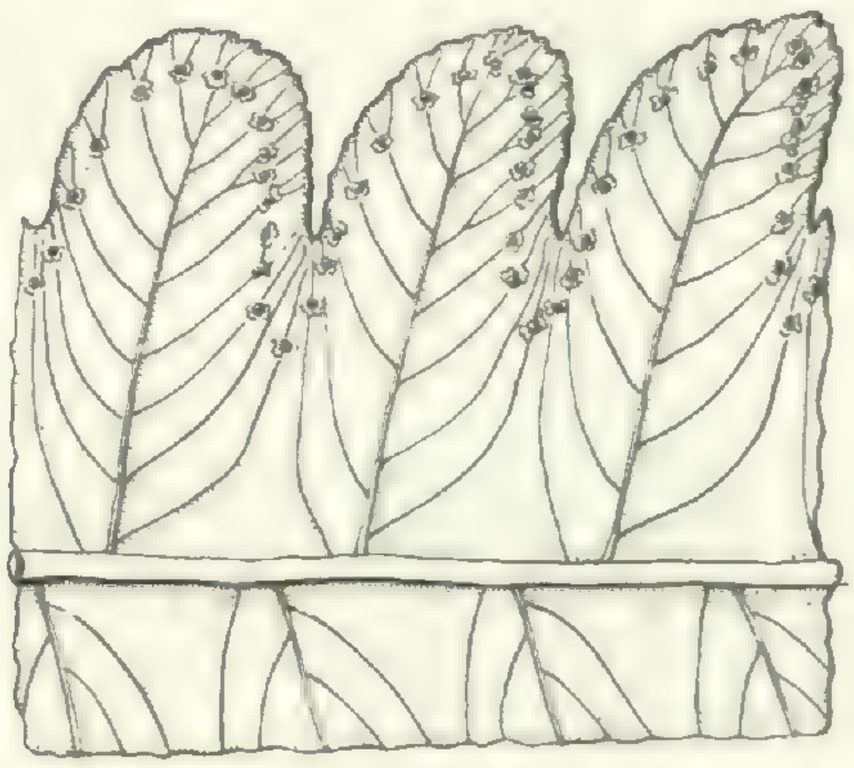
Cyathea asperata Sod.
C. aspidiiformis Domin, *Cyathea aspidioides* Sod., not (Bl.) Moritz.
C. aurea Karst.
C. Boryana (Kuhn) Domin, *Hemitelia Boryana* Kuhn.
C. brachypoda Sod.
C. castanea Baker.
C. catacampta Alston.

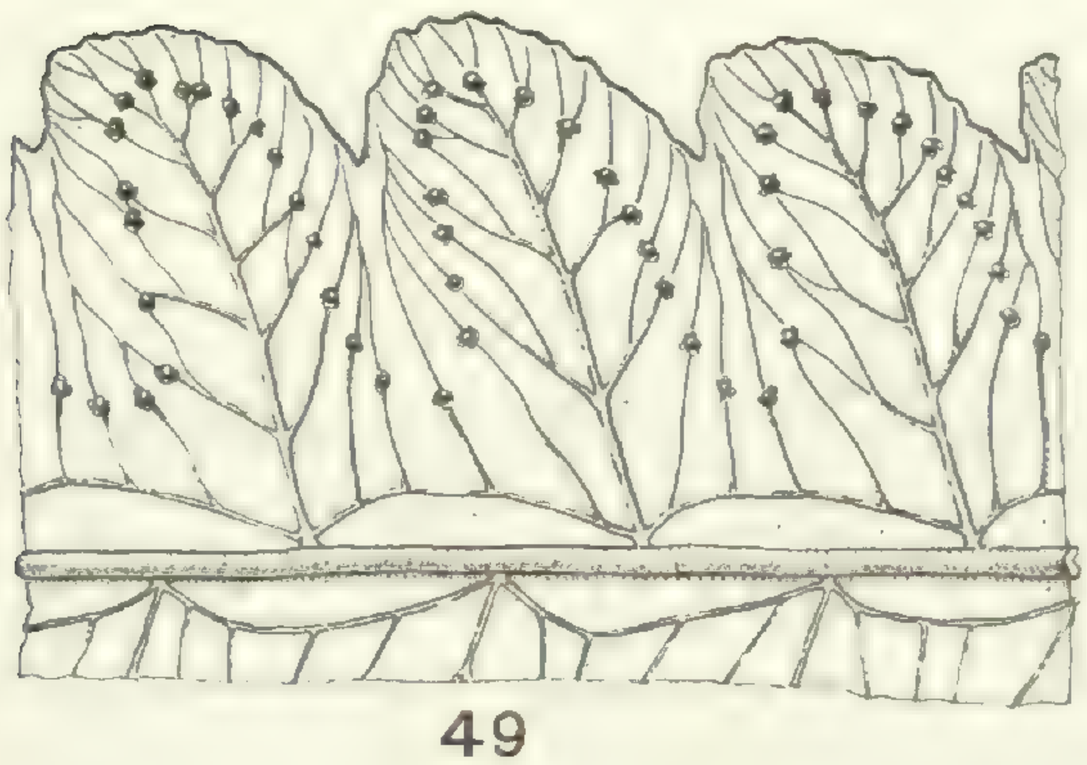












FIGS. 44–50. CYATHEA and CNEMIDARIA. FIGS. 44–46. CYATHEA, portions of petiole scales, all × 90: 44, *Cy. puberula, Cuatrecasas 18186,* US. 45, *Cy. platylepis, Schultes & Cabrera 15079,* GH. 46, *Apex, Cy. parvula, Proctor 5513,* GH. FIGS. 47–50. CNEMIDARIA. FIG. 47. Portion of petiole scale, *Cn. spectabilis, Britton et al. 1238,* × 30, NY. FIGS. 48–50. Portions of pinnae showing venation, receptacles and indusia: 48, *Cn. bella, Hort. Lips.* × 1, MO. 49, *Cn. speciosa, Killip & Smith 24536,* × 1–1/2, GH. 50, *Cn. Ewanii, Ewan 16729,* × 1–1/2, US.

C. columbiana Domin, *Hemitelia obscura* Mett., not *Cyathea obscura* (Bedd.) Copel.
C. Copelandii Luerrs. (Ilha Trindade).
C. corallifera Sod.
C. decorata (Maxon) Tryon, comb. nov., *Hemitelia decorata* Maxon, Jour. Arn. Arb. 27:439. 1946.
C. divergens Kze.
C. ebenina Karst.
C. frondosa Karst.
[*Cyathea fulva* Sod.=**Cyathea Sodiroi**].
C. Herzogii Rosenst.
C. leucolepismata Alston.
C. meridensis Karst.
C. Mettenii Karst.
C. microphylla Mett.
C. muricatula Sod.
C. nitens Sod.
[*Hemitelia obscura* Mett.=**Cyathea columbiana**].
C. ocanensis Baker.
C. ochroleuca Sod.
C. parvifolia Sod.
C. petiolulata Karst.
C. pilosa Baker.
C. platylepis (Hook.) Domin, *Hemitelia platylepis* Hook.
C. puberula Sod.
C. rupestris Maxon.
C. schanschin Mart.
C. Sodiroi C.Chr., *Cyathea fulva* Sod., not (Mart. & Gal.) Fée.
C. squamipes Karst.
C. straminea Karst.
C. subinermis Sod.
C. tungurahuae Sod.
C. vestita Mart.
C. Weatherbyana (Morton) Morton, *Hemitelia Weatherbyana* Morton (Galápagos Isls.).

8. Cnemidaria

Cnemidaria Presl, Tent. Pterid. 56. 1836. Type: *Cnemidaria speciosa* Presl.

Cnemidopteris Reichenb. Deutsche Botaniker 1 (Repert, Herb. Nomencl. Gen. Pl.), Abtheil. 2:148, 235. 1841, is an illegitimate correction of the name *Cnemidaria* Presl.

Microstegnus Presl, Gefässbündel Stipes der Farrn, 45. 1847 (preprint from Abhandl. böhm. Ges. V, **5**:353. 1848). Type: *Microstegnus grandifolius* (Willd.) Presl (*Cyathea grandifolia* Willd.) = *Cnemidaria grandifolia* (Willd.) Proctor.

Hemistegia Presl, Gefässbündle Stipes der Farrn, 46. 1847 (preprint from Abhandl. böhm. Ges. V, **5**:354. 1848). Lectotype: *Hemistegia Kohautiana* (Presl) Presl = *Cnemidaria Kohautiana* Presl.

Actinophlebia Presl, Gefässbündel Stipes der Farrn, 47. 1847 (preprint from Abhandl. böhm. Gas. V, **5**:355. 1848). Type: *Actinophlebia horrida* (L.) Presl (*Polypodium horridum* L.) = *Cnemidaria horrida* (L.) Presl.

Petiole smooth to tuberculate, or rarely with corticinate spines, lacking trichomes; petiole *scales* (especially on the abaxial side) more or less appressed, attached at one point of a pseudopeltate or peltate base, structurally marginate, with a narrow to broad margin of cells different in orientation, size, shape, and usually in color from those of the central portion, lacking dark setae, the apex rounded to filamentous; *minute indument* of the petiole, when present, of appressed trichomidia; *costa* usually glabrous above, rarely pubescent; *veins* forming areolae along the costa (sometimes beyond), or free and in lobed or pinnatifid segments, the basal vein on each side connivent to the base of the sinus; *indusium* present, hemitelioid.

Cnemidaria (Figs. 13, 47–50) is an American genus of about 40 species. It represents a strong evolutionary line which, in the more advanced species, has developed reduced lamina architecture, areolate venation (Figs. 49–50), an acaulescent habit and equatorial pores on the spores. While evolution has occurred in these characters, the indusium has maintained an essentially uniform hemitelioid form. The petiole scales (Fig. 47) are similar in cellular differentiation to those of *Trichipteris* and *Cyathea* and they are discussed in detail under *Cyathea*. In most species there is a relatively broad petiole scale with a dark central portion and broad whitish margins. The chromosome number of $n=69$ has been reported for *Cnemidaria horrida* by Walker (1966).

The following list of species will serve as examples of the genus. It does not include those in which problems of taxonomy or nomenclature are known.

WEST INDIES

Cnemidaria grandifolia (Willd.) Proctor, *Hemitelia grandifolia* (Willd.) Spreng.

Cn. horrida (L.) Presl, *Hemitelia horrida* (L.) Spreng.

Cn. Kohautiana Presl, *Hemitelia Kohautiana* (Presl) Kze.

Cn. obtusa (Kaulf.) Presl, *Hemitelia obtusa* Kaulf.

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Cnemidaria arachnoidea (Maxon) Tryon, comb. nov., *Hemitelia arachnoidea* Maxon. Contrib. U. S. Nat. Herb. **16**:34. 1912 (*Cnemidaria arachnoidea* Underw., in synon.).

Cn. chiricana (Maxon) Tryon, comb. nov., *Hemitelia chiricana* Maxon, Contrib. U. S. Nat. Herb. **16**:33. 1912.

Cn. choricarpa (Maxon) Tryon, comb. nov., *Hemitelia choricarpa* Maxon, Contrib. U. S. Nat. Herb. **16**:40. 1912.

Cn. conformis (Tryon) Tryon, comb. nov., *Hemitelia conformis* Tryon, Rhodora **62**:1. 1960.

Cn. contigua (Maxon) Tryon, comb. nov., *Hemitelia contigua* Maxon, Contrib. U.S. Nat. Herb. **16**:32. 1912 (*Cnemidaria contigua* Underw., in synon.).

Cn. decurrens (Liebm.) Tryon, comb. nov., *Hemitelia decurrens* Liebm. Vid. Selsk. Skr. V, 1:286. 1849.

Cn. grandis (Maxon) Tryon, comb. nov., *Hemitelia grandis* Maxon, Contrib. U. S. Nat. Herb. **16**:37. 1912.

Cn. mutica (Christ) Tryon, comb. nov., *Hemitelia mutica* Christ, Bull. Soc. Bot. Genève II, 1:233. 1909.

Cn. petiolata (Hook.) Copel., *Hemitelia petiolata* Hook.

Cn. rudis (Maxon) Tryon, comb. nov., *Hemitelia rudis* Maxon, Contrib. U. S. Nat. Herb. **17**:413. 1914.

Cn. subglabra (Maxon) Tryon, comb. nov., *Hemitelia subglabra* Maxon, Contrib. U. S. Nat. Herb. **16**:36. 1912 (*Cnemidaria subglabra* Underw., in synon.).

SOUTH AMERICA

Cnemidaria abitaguensis (Domin) Tryon, comb. nov., *Hemitelia abitaguensis* Domin, Kew Bull. 1929: 215.

Cn. amabilis (Morton) Tryon, comb. nov., *Hemitelia amabilis* Morton, Fieldiana Bot. **28**:10. 1951.

Cn. bella (Mett.) Tryon, comb nov., *Hemitelia bella* Mett. Fil. Hort. Bot. Lips. 110. 1856.

Cn. dissimilis (Morton) Tryon, comb. nov., *Hemitelia dissimilis* Morton, Fieldiana Bot. **28**:8. 1951.

Cn. Ewanii (Alston) Tryon, comb. nov., *Cyathea Ewanii* Alston, Jour. Wash. Acad. Sci. **48**:231. 1958.

Cn. integrifolia (Kl.) Tryon, comb. nov., *Hemitelia integrifolia* Kl. Linnaea **18**:539. 1844.

Cn. Karsteniana (Kl.) Tryon, comb. nov., *Hemitelia Karsteniana* Kl. Allgem. Gartenzeit. **20**:42. 1852.

Cn. Lindenii (Hook.) Tryon, comb. nov., *Hemitelia Lindenii* Hook. Icon. Pl. t. 706. 1848, *Cyathea speciosa* Willd. (not *Cnemidaria speciosa* Presl) *Hemitelia speciosa* (Willd.) Kaulf.

Cn. nervosa (Maxon) Tryon, comb. nov., *Hemitelia nervosa* Maxon, Jour. Wash. Acad. Sci. **34**:309. 1944.

Cn. quitensis (Domin) Tryon, comb. nov., *Hemitelia quitensis* Domin, Kew Bull. 1929: 215.

Cn. roraimensis (Domin) Tryon, comb. nov., *Hemitelia roraimensis* Domin, Kew Bull. 1929: 216.

Cn. speciosa Presl, *Hemitelia subincisa* Kze. (nom. nov. for *Cnemidaria speciosa* Presl, not *Hemitelia speciosa* (Willd) Kaulf.).

[*Hemitelia speciosa*=**Cnemidaria Lindenii**].

Cn. spectabilis (Kze.) Tryon, comb. nov., *Hemitelia spectabilis* Kze. Linnaea **21**:233. 1848.

[*Hemitelia subincisa*=**Cnemidaria speciosa**].

Cn. Uleana (Sampaio) Tryon, comb. nov., *Hemitelia Uleana* Sampaio, Bol. Mus. Nac. Rio Janeiro **1**:65. 1923.

LITERATURE CITED

BOWER, F. O. 1926. The Ferns, vol. 2. Cambridge University Press.

BROWNLIE, G. 1961. Additional chromosome numbers—New Zealand ferns. Trans. Roy. Soc. New Zealand Bot. **1**:1–4.

CHRISTENSEN, C. 1938. Filicinae (Chapter 20), Verdoorn (Ed.), Manual of Pteridology. Martinus Nijhoff.
DEWOLF, G. 1953. On the sub-division of the Cyatheaceae. M. Sc. Thesis, University of Malaya.
HOLTTUM, R. E. 1957. The scales of Cyatheaceae (with special reference to *Schizocaena* J. Sm.). Kew Bull. **1957**:41–45.
———. 1963. Cyatheaceae. Flora Malesiana II, 1 (2): 65–176.
———. 1964. Tree-ferns of the genus *Cyathea* Sm. in Asia (excluding Malaysia). Kew Bull. **19**:463–487.
———. 1965. The tree-ferns of the genus *Cyathea* in Australasia and the Pacific. Blumea **12**:241–274.
——— & U. SEN, 1961. Morphology and classification of the tree-ferns. Phytomorphology **11**:406–420.
MANTON, I. & W. A. SLEDGE. 1954. Observations on the cytology and taxonomy of the Pteridophyte flora of Ceylon. Phil. Trans. Roy. Soc. London, Ser. B, **238**:127–185.
RIBA, R. 1969. The *Alsophila Swartziana* complex (Cyatheaceae). Rhodora **71**:7–17; *and* Revision monografica del complejo *Alsophila Swartziana* Martius (Cyatheaceae). Ann. Instit. Biol. Univ. Nac. Autón. México, 38, Ser. Bot. (1): 61–100. "1967."
ROY, S. K. & R. E. HOLTTUM. 1965. Cytological and morphological observations on *Metaxya rostrata* (H.B.K.) Presl. Amer. Fern Jour. **55**:160–164.
SEN, U. 1964. Importance of anatomy in the phylogeny of tree ferns and their allies. Bull. Bot. Soc. Bengal **18**:26–34.
STEARN, W. T. 1954. Notes on some botanical works. Jour. Soc. Bibl. Nat. Hist. **3**:13–16.
TARDIEU-BLOT, M. 1941. Sur les aphlebia des Cyathéacées malgaches. Bull. Soc. Bot. France **88**:522–531.
———. 1951. Cyathéacées. Humbert, Fl. Madagas. Comores. 4e famille.
———. 1953. Les Ptéridophytes de l'Afrique intertropicale Française. Mém. Instit. Franc. Afr. Noire 28.
WALKER, T. G. 1966. A cytotaxonomic survey of the Pteridophytes of Jamaica. Trans. Roy. Soc. Edinb. **66**:169–237.

A MONOGRAPH OF THE FERN GENUS ERIOSORUS[1]

ALICE F. TRYON

Eriosorus, a genus of tropical American ferns, is perhaps more familiarly known under the older name, *Gymnogramma*, stemming from Hooker's Synopsis Filicum (1868) which included nearly a hundred species. Underwood (1902), in his series on genera of American ferns, attacked Hooker's treatment as "the most unaccountable and unnatural collection of misfits that ever figured in the pages of a treatise on systematic botany." Although Hooker's treatment was indeed unnatural, Underwood's criticism was unduly caustic since Hooker did divide *Gymnogramma* into six sections, and the species now under *Eriosorus* were, for the most part, treated under *Eugymnogramma*.

The following is an account of publications treating significant groups of the species now in *Eriosorus*, as well as the most useful and recent generic classifications. The essential data on the taxonomic history of each of the species are found in the synonymy.

As with much of systematic botany, the initial critical work came from Sweden. The first handbook of ferns by Olof Swartz (1806) included *Grammitis cheilanthoides* from Tristan da Cunha (erroneously reported from Mauritius). Documented specimens from these islands were made by Aubert du Petit-Thouars in 1793. In the text of his work, Petit-Thouars (1808) described the species as *Asplenium filipendulaefolium*, but the illustration is named *Grammitis cheilanthoides* Sw. Apparently Petit-Thouars learned of the earlier name while his work was in preparation.

Studies of American tropical plants were greatly stimulated by the explorations and publications of Alexander von Humboldt. Near Caracas, Venezuela, he and Bonpland collected two species of this group. These specimens were classified by Niçaise Desvaux (1827) under the new genus, *Gymnogramma*. He combined them with the earlier species described by Swartz, in the genus *Grammitis*, on the basis of the sporangia without indusia disposed along the veins. Unfortunately, he also included *Gymnogramma rufa* (L.) Desv., which is the type of the earlier genus *Gymnopteris*, thus *Gymnogramma* is now considered to be a superfluous name, as has been already noted by A. Tryon (1963).

Specimens, from the rich collections sent from Ecuador to Kew

[1] The work has been supported by National Science Foundation Grant GB-1693.

by William Jameson, were the basis for the new genus *Jamesonia*, described by William Hooker and Robert Greville in the Icones Filicum (1827–1831). Shortly after proposing this genus, they described two new species under *Gymnogramma*, based on the Jameson collections, and these are now considered to represent hybrids involving *Jamesonia*.

Eriosorus was proposed by Antoine L. Fée (1852), not as a replacement for *Gymnogramma*, but as a new segregate genus. On the basis of many approximate and mostly confluent sori, it it was included with *Jamesonia* and five other genera under *Polypodiaceae*, subtribe *Cheilantheae* in the group *Eucheilantheae*. *Eriosorus rufescens* (as *Gymnogramma*) was proposed in the same work and included in subtribe *Hemionitideae*, in the group *Leptogrammeae* which also included *Pterozonium*, on the basis of the sori being equivalent in number to the veins. *Anogramma* was also treated in the same publication, and under this name Fée proposed a new species of *Eriosorus* as *Anogramma Ottonis*. Thus, *Eriosorus* was first presented, in a restricted sense but with several species now recognized as belonging to it, under two other genera.

Gustav Kunze combined *Gymnogramma* under *Jamesonia*, and noted the similarities of the genera in the detailed description of *Jamesonia hispidula* in his Farmkraüter (1846). This concept was reversed by Georg Mettenius in his floristic treatment of the Filices (1864) in which he used *Gymnogramma* and placed *Jamesonia* in synonymy. This early work on the Colombian flora was elaborated by Herman Karsten (1857–1869). He treated seven species under *Gymnogramma*, based on his own collections and field observations. His specimens from the vicinity of Bogotá represent some of the difficult variant forms which now appear to be hybrids. The most complete study of those species now included in *Eriosorus* was made by Maximilian Kuhn in his work on the *Chaetopterides* (1882). Both *Jamesonia* and *Eriosorus* are included under *Psilogramme*, the former under subgenus *Jamesonia* and the latter under *Eupsilogramme* which included 24 species, 16 of which are recognized here.

Lucien M. Underwood (1902) followed this use of *Psilogramme* in his review of Hooker's application of the name *Gymnogramma*. The name *Psilogramme* was also used by William R. Maxon in his work on the North American species (1915). Edwin B. Cope-

land revived the earlier name, *Eriosorus,* in his Genera Filicum (1947) as being a genus of 35 species, 14 of which he lists. This name has been followed since then, as in the study of the species in Costa Rica by Edith Scamman (1962), and in the work on the Ferns of Peru by R. Tryon (1964). I prefer to follow Carl Christensen's classification (1938) of the *Polypodiaceae* until more facts are known about the relationships of the families. In this, *Eriosorus* (as *Gymnogramma*) was placed in the subfamily *Gymnogrammeoideae,* the tribe *Gymnogrammeae* and in the group of the *Chaetopterides* which includes *Jamesonia, Pterozonium* and three other genera. In the most recent classification by Rudolfo E. G. Pichi-Sermolli (1966) *Eriosorus* is included in the new family *Hemionitidaceae,* between *Pterozonium* and *Jamesonia,* in the tribe *Jamesonieae* with four other genera. A larger group of genera, including *Pityrogramma* and *Anogramma* are treated in the tribe *Hemionitideae.*

On the basis of this study and that of *Jamesonia* (1962), as well as the work on the related groups, *Pityrogramma* and *Anogramma,* by Rolla Tryon (1962) and of *Pterozonium* by David Lellinger (1967), it appears that *Eriosorus* represents the least advanced element among these five, mainly American, genera. *Eriosorus, Jamesonia* and *Pterozonium* form a closely related group on the basis of many similarities such as the pattern of venation, soral arrangement, alignment and structure of the sporangium, indument and spores. In these characters they are sufficiently distinct from the Old World genera *Syngramma, Craspedodictyum* and *Taenitis* to represent an independent evolutionary line. *Anogramma* and *Pityrogramma* are not as closely related but similarities of the sorus, sporangia, spores and lamina indument indicate that they can be associated with the previous three. Several cytological reports for these genera have established a base number of $x = 29$ for *Anogramma,* which is the same as that here suggested as the base number for *Jamesonia* and *Eriosorus* on the basis of hexaploid or higher counts. From a number of counts, *Pityrogramma* appears to have a base number of $x = 30$. However, the recent report by Walker (1966) of $n = 58$ for *Pityrogramma trifoliata* (as *Trismeria*) in Jamaica, along with evidence for hybrids between this and *Pityrogramma* as proposed by Rolla Tryon (1962) suggest that *Pityrogramma* has base numbers of both 29 and 30.

Eriosorus is regarded as the least advanced among these five genera as is evident from the less elaborated spore sculpture, the simple form of rhizome indument, unspecialized leaf form in several species and in the spathulate form of the gametophyte. There is a close relationship between this genus and *Jamesonia* and it is apparent that the latter has been derived from more than one element in *Eriosorus*. The relationship to *Pterozonium* is not as close and is without clear lineal derivation.

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Evolutionary Trends

Eriosorus represents a relatively old group among genera of the *Polypodiaceae*. This is made evident by the occurrence of exindusiate sori which follow the veins, spathulate gametophytes, a high polyploid level, a fossil record of the spores and a broad geographic range. Hybridization appears to have obscured the broader lineal evolutionary relationships in the genus. Most of the species can be associated in groups of two or three closely allied members as shown in Fig. 1. This chart summarizes the species groups, the major levels of specialization and also affinities with other genera. More detailed relationships are noted in the species treatments and in discussions on the cytology, geography and morphology.

Associations that can be most clearly established are indicated by heavy lines. The species groups are arranged in three levels: those at the lowest, most generalized level have well developed elongate-triangular leaves, simple rhizome trichomes and deep brown spores; the highest level shows two major trends in specialization of the leaves—complex, scandent ones and compact, linear forms; the central level consists of groups intermediate to the two extreme ones.

The most generalized level is best represented by *Eriosorus myriophyllus* and *E. congestus* with their unspecialized leaves, simple rhizome trichomes and deep brown spores. *Eriosorus*

Sellowianus is close to the former species, but has more constricted leaves and is confined to drier sites in Minas Gerais. The above three species are geographically peripheral to the main Andean center of the genus. The broad range of *E. myriophyllus* in Brazil, at the lowest altitudinal range for the genus, suggests a possible center here prior to Andean speciation. The occurrence of *E. congestus* in Costa Rica suggests an earlier migration of an unspecialized form northward from South America. Hexaploidy in this species and in *E. myriophyllus* shows that a high polyploid level has been attained in these generalized species.

At the intermediate level, no strong association can be established between the five main species groups. Affinities within the groups are indicated by heavy connecting lines on the chart. There are especially close relationships between *E. hirtus* and *E. hispidulus* as shown by similarities in leaf architecture, black rhizome bristles and tan spores. The group of *E. aureonitens-accrescens-Stuebelii* is characterized by dense tomentum on the leaves. Relationships in this group may be complicated by hybridization because the species occur together and the latter two have irregular spores. The group of *E. Wurdackii-insignis-Orbignyanus*

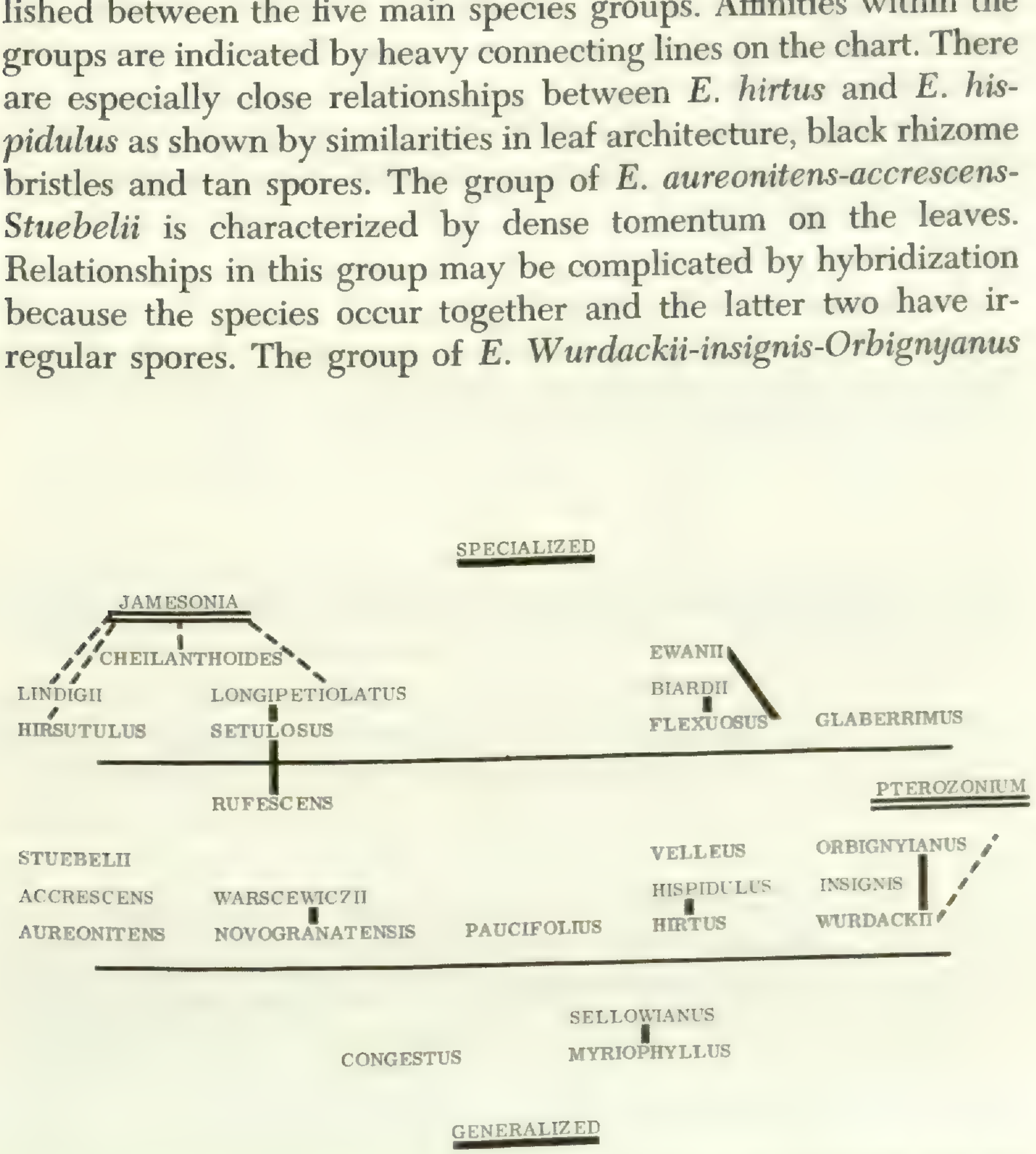


FIG. 1. Chart of the evolutionary trends. The taxa arranged as noted under that topic in the text.

has similar sori, restricted to marginal bands and pinnae departing from the rachis at angles greater than 90 degrees. *Eriosorus Wurdackii* is the least specialized of this group and supplies a link with this genus and *Pterozonium*. Relationships with *Pterozonium* are shown in several characters, such as the sub-marginal sori, firm pinna texture, deep brown trichomes confined mainly to the sorus, and vein ends terminating short of the margin. *Pterozonium reniformis* and *P. brevifrons*, two of the most widely distributed species, occur in northern Peru, and the latter has been collected by Wurdack in the same area as *Eriosorus*.

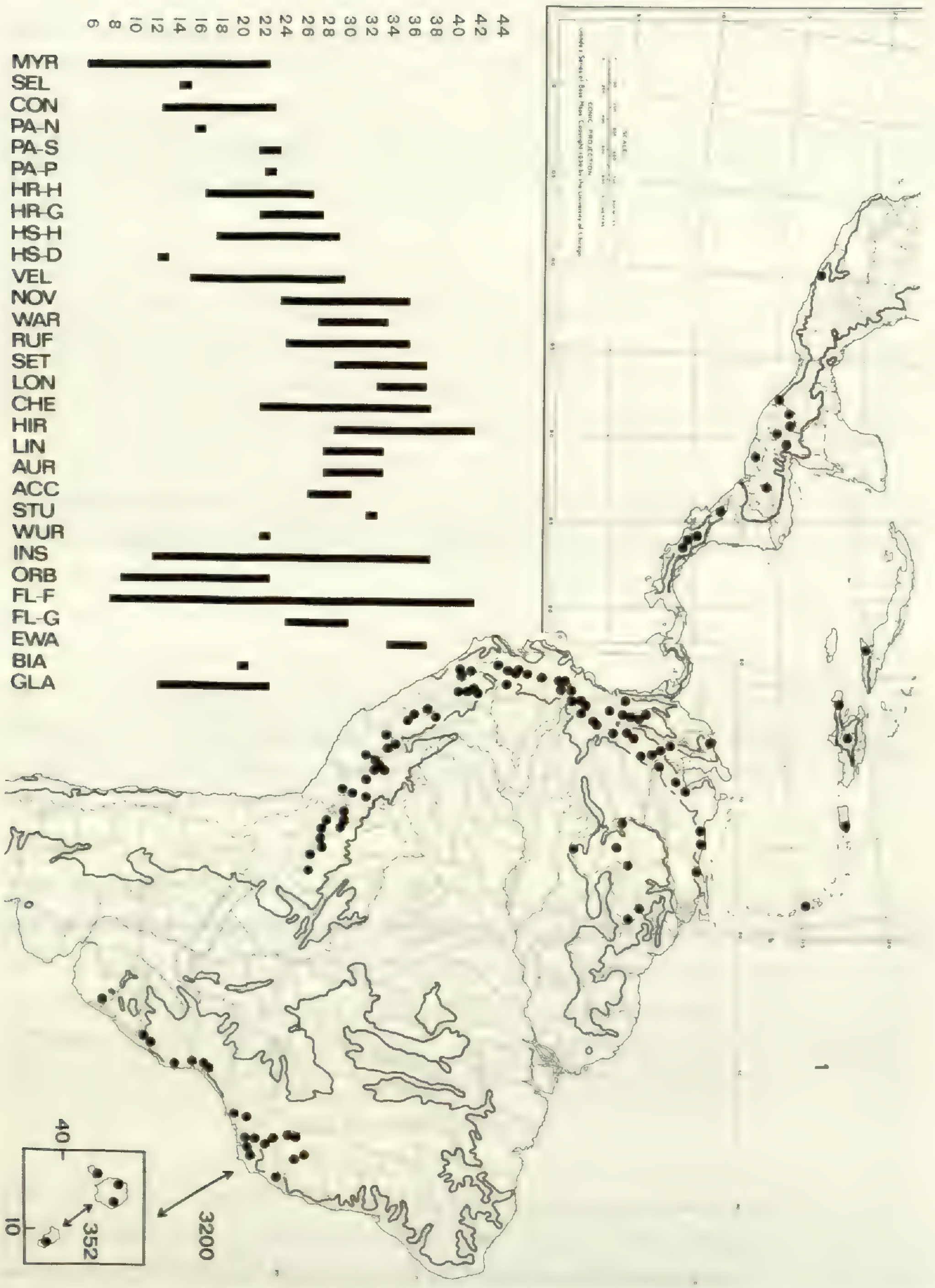
There are two trends in leaf form among the most specialized species. The scandent one is best represented by *Eriosorus flexuosus*. The broad, black rhizome bristles and light tan spores also show specialization in characters other than the leaves. *Eriosorus flexuosus* is one of the most dynamic species ecologically, as shown by its broad geographic distribution and wide altitudinal range. It occurs with *Eriosorus Biardii* in Brazil and appears closely allied to it because of similarities in the fractiflex rachises and slender, bifurcate ultimate segments. *Erisorus Ewanii* is a remarkable species, also close to *E. flexuosus*. It represents an intermediate between the scandent and linear-leaved forms, but exhibits several unique characters as noted in the species discussion.

The second evolutionary trend at the most specialized level is the reduction of the leaves to linear forms. It is from this group that *Jamesonia* has evolved, and here there are no clear morphological disjunctions between the genera. There are several hybrids and variants, noted in the species treatments, which involve *Jamesonia* and *Eriosorus*. *Eriosorus cheilanthoides* is geographically the most dynamic species of the linear-leaved group with the widest distribution in the genus, reaching the most remote island in the South Atlantic. Its relationships to other 1-pinnate species, such as *E. hirsutulus* and *E. Lindigii*, are not clear, but these may be involved in hybridization with *E. cheilanthoides* at the lower polyploid levels. These species are involved with *Jamesonia*, and variants implicating *Jamesonia imbricata*, *J. rotundifolia* and *J. bogotensis* are noted in the species treatments. A second series of linear-leaved species that represents another independent connection with *Jamesonia* includes *E. setulosus* and *E. longipetiolatus*. They are related to *E. rufescens* at the intermediate level of specialization, and to a group of species allied to *J. verticalis*.

Geography

Morphological diversity within this genus suggests that the amount of evolution involved has required considerable time. A few fossil records of the spores document its occurrence in the Pleistocene and possibly the Oligocene. Spores of *Eriosorus cheilanthoides* were described from peat cores on Tristan da Cunha and Gough Island in the South Atlantic by Hafsten (1960). On Tristan these are at the lowest level of the core, below 2.8 m. and two levels above this. On Gough Island the record is more continuous from 4.3 m. up to 0.3 m. This profile was correlated with a radio-carbon-dated monolith, dated at 4720 ± 130 B. P. *Eriosorus* spores are found below this dated level and thus have probably existed there for at least 5000 years. Hafsten's excellent photographs of subfossil spores from 3.5 m. on Gough show the prominent equatorial flange with projecting angles characteristic of modern material. Similar spores are identified by van der Hammen and Gonzalez (1960) as *Jamesonia* but these cannot be distinguished from those of *Eriosorus*. These samples were taken near Bogotá, Colombia and the lowest level represents Pleistocene deposition. The base of the core was C_{14} dated at 21,900 (± 600) B.C. and was interpreted as the last part of a cold phase, probably of the Würm stage of the Pleistocene. The profile shows a nearly continuous record of these spores from the lowest level at 32 m. up to near the surface. They are the most abundant spores of the pteridophytes included in their sample, except for "Cyatheaceae," and suggest that these plants were flourishing during most of the period. The photographs certainly represent either *Eriosorus* or *Jamesonia* spores. At the present time both genera are frequent in the vicinity of the Sabana de Bogotá and it is quite possible that the spore sample may represent a mixture of both. A single spore of *Jamesonia* is reported by Briggs and Graham (A. Graham, pers. comm. 1969) from the San Sebastian formation in Puerto Rico and is dated Middle Oligocene. If it can be identified as this complex with certainty, it more likely represents *Eriosorus* which is known from the Luquillo Mts. in Puerto Rico. The evolutionary development of *Eriosorus* and its broad geographic range do imply a considerable period of development and a mid-Tertiary record would not be unexpected.

The geographic distribution of the species also provides some information on the evolutionary history of the genus. The species



MAP 1. Distribution of *Eriosorus* and graph of altitudinal ranges. Map with 1000 foot contour in outline, inset of South Atlantic islands, Tristan da Cunha 3200 km. se. of Brazil, Gough 352 km. se. of Tristan. Altitudinal ranges at 200 m. intervals, 600–4200 m. the taxa abbreviated by the first two or three letters, the varieties by a dash and the first letter.

are mainly in cool, moist highlands. The general range is shown on Map 1 with the 1000 foot (305 m.) contour in outline. The altitudinal range is between 600–4200 m. The graph accompanying the map shows altitudinal ranges of the species. The altitudes are usually expressed as ranges on the collections and the whole range is arbitrarily incorporated in the bars for each of the taxa. More than half of the taxa occur above 2200 m. and only three are wholly below 1800 m.

The general geographic range of *Eriosorus* extends from Santa Cruz in central Bolivia, north along the Andean Cordillera and Central American highlands to the high pine-oak forest in Guerrero, Mexico. In Venezuela, it occurs from the Sierra Nevada eastward along the mountains bordering the Caribbean to Sucre. It is disjunct on several of the sandstone massifs in Venezuela and on Roraima in British Guiana. In Brazil, the genus extends from Minas Gerais south in the highlands to Cerro Largo, Uruguay. Species of the genus are known in the Lesser Antilles in Dominica and also in the Greater Antilles in Cuba, Hispaniola and Puerto Rico. The most disjunct stations are in Tristan da Cunha and Gough, some 2000 miles east of South America.

The species are concentrated in Brazil, the Andes and Costa Rica. Of the six Brazilian species, four endemics are relatively wide-ranging in southeastern Brazil. Of these, *Eriosorus myriophyllus* is most widely distributed and occurs at 600 m., the lowest altitude reported for the genus. *Eriosorus Sellowianus* is a more specialized form, restricted to Minas Gerais. The other two endemic species, *E. Biardii* and *E. insignis*, are also more specialized and are more closely related to the Andean species than those of Brazil. *Eriosorus flexuosus* and *E. cheilanthoides*, the two species representing the most specialized forms in the genus and those having the widest geographical range, are confined to single stations at high altitudes in Brazil. They are considered to be more recent migrants than the above-mentioned Brazilian species, and are found in the Andean region. *Eriosorus cheilanthoides* certainly arrived on Tristan by long distance dispersal from eastern Brazil after the last half of the Pleistocene when the island was first available for colonization. This also suggests that the species might have migrated across the continent from the Andes in the same manner.

The largest concentration of species, including 19 taxa, is in the Andean region. Ten of these occur at high altitudes, mainly above

3000 m., and most of them have reduced, linear leaves and local ranges and five of them are endemic in Colombia. They are exemplified by *Eriosorus longipetiolatus*, which has very reduced, jamesonioid leaves. This species occurs on two islolated páramos of southern Colombia in conjunction with species of *Jamesonia* and *E. setulosus* from which it is possibly derived by hybridization. In the Andes of Peru there are three endemic species, each occurring in the north around Chachapoyas. *Eriosorus Wurdackii* is known only from there and *E. Stuebelii* and *E. accrescens* appear again in the southernmost department of Puno.

The concentration of species with reduced leaves at high altitudes in the Andes represents more than one evolutionary line. A group of six species with large, scandent leaves is also mainly Andean. The latter occur at a lower altitude, have greater altitudinal range and represent different evolutionary elements. Specialized characters such as glandular, tomentose or coriaceous conditions of the leaves or light colored spores are also derived features of Andean species that have moved north into Mexico and east into Venezuela. This diversity of forms in the Andean region may reflect the considerable climatic fluctuations which occurred during the Pleistocene.

The Central American species are mostly concentrated on the higher volcanos of Costa Rica. The four species which occur there are more closely related to South American species than to each other. *Eriosorus congestus*, the most frequently found, is usually very abundant at lower altitudes than the others in Costa Rica. *Eriosorus Warscewiczii*, which occurs at the highest altitudes, is also reported from and is closely related to species of Colombia.

In the Caribbean region, there is evidence of independent introductions in the Lesser and Greater Antilles. It seems likely that the glandless form of *Eriosorus hispidulus* on Dominica came from a population in northern Venezuela rather than from the glandular ones of Puerto Rico or Guatemala. *Eriosorus flexuosus*, the other species on Hispaniola, and *E. hirtus* of Cuba, probably also came from northern Venezuela, where they are more widely distributed at present, rather than from more limited stations in Central America or Mexico. However, it is peculiar that both *E. hirtus* and *E. hispidulus* occur in Guatemala but are not known from Costa Rica. Their disjunct ranges suggest that they were more widely distributed in the past.

There are no strong phyletic lineages evident in this genus as have been shown in other groups in the American tropics such as *Pellaea, Doryopteris* and *Lindsaea*. There are aggregates of two or three closely related species without strong connections between them. The morphological diversity and disconnected elements in *Eriosorus* can probably be correlated with the pronounced climatic and ecological changes that occurred, particularly in the Andean region, during the Pleistocene. The fluctuations during this period would be effective forces influencing the migration, isolation and extinction of populations and would also provide the environmental conditions for hybridization which is characteristic of the genus. Observations at sites where *Eriosorus* occurs in montane areas of Costa Rica and Colombia show that conditions suitable for hybridization are produced where man has been active in eliminating the forests by burning and lumbering.

Cytology

The existence of both 6-ploid and 12-ploid chromosome numbers proves that polyploidy occurs in *Eriosorus*. The presence of plants with ca. 174 largely unpaired chromosomes at meiosis shows an intermediate condition between the two polyploid levels. It demonstrates a stage prior to doubling of chromosomes in the sequence which has resulted in high chromosome numbers in this genus. The illustrations of meiotic cells, shown in Fig. 2, and the chromosome numbers included in Table 1, were obtained from young sporangia, prepared in the field, in a standard fixative of 3:1 alcohol and glacial acetic acid. These were stored under refrigeration from one to six months, and then stained in aceto-carmine, as described by Manton (1950). Photographs were made from these preparations which were made permanent by freezing with solid CO_2, and mounted in diaphane. The cytological records for *Eriosorus* and *Jamesonia*, including literature records, are summarized in Table 1.

The prevalence of morphologically discrete species in *Eriosorus* and those in *Jamesonia* with meiotic chromosome numbers of 87 suggests that these levels have been attained in a uniform system. The number is regarded as representing a hexaploid level and may possibly be derived from other genera at lower levels. However, on consideration of the wide diversity of morphological

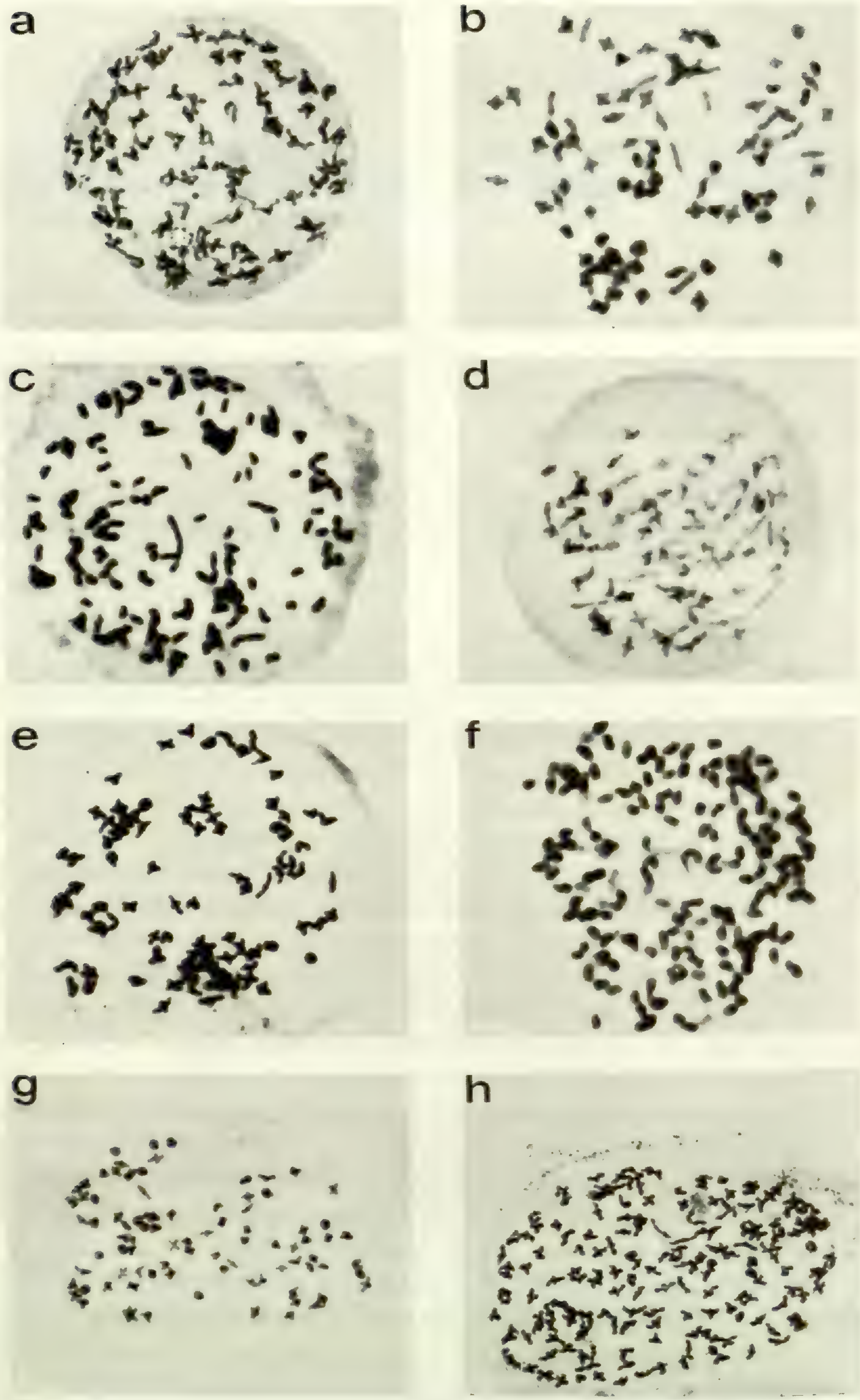


FIG. 2. For legend, see opposite page.

types, particularly among the Andean species, and the record of two ploidy levels within the genus, it seems likely that the lower levels may still be found among the Andean species.

The meiotic chromosome number of 174 for *Eriosorus cheilanthoides* was first reported by Manton & Vida (1968) and was interpreted by them as 12-ploid. They regarded this unusually high number in the Tristan plants as confirmation of Christensen's view that the species is an endemic on those islands. They also noted the special need for an examination of Andean plants, which I had regarded (A. Tryon, 1966) as similar to those on Tristan. The chromosome count presently reported from a collection of *E. cheilanthoides* from Mt. Itatiaia, the highest peak in eastern Brazil, as $n=174$ confirms the close relationship of the Tristan plants to the continental ones. On Itatiaia, *E. cheilanthoides* grows in close association with *Jamesonia brasiliensis* and there are specimens intermediate between these species. Cytological fixations of these unfortunately did not yield definitive results. This dodecaploid level of $n=174$ apparently has been derived from a lower hexaploid and the latter from doubling of the triploid stage. In turn, the triploid has undoubtedly originated from crosses between the diploid and tetraploid which are based on the monoploid, x=29. This scheme is supported by the independent interpretation by Manton & Vida of *E. cheilanthoides* as a 12-ploid based on x=29, which they made prior to the discovery of hexaploids. The high somatic chromosome number, $2n=348$ in *E. cheilanthoides,* supports its disposition as a derived species as shown in several morphological characters noted elsewhere.

A precise count could not be determined for *Eriosorus myriophyllus* from Brazil, but from the general volume of paired chromosomes in meiotic cells the number seemed to be on the order of a hexaploid. Cytological investigation of this species, which grows at relatively low altitudes, is of interest since it represents the most generalized form in the genus.

In my revision of the genus *Jamesonia, J. bogotensis* from Páramo Chisaca in Colombia was reported as $n=87$ at meiosis. The present report of the same number for *J. Scammanae* from

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FIG. 2. Photographs of chromosome squashes from permanent acetocarmine preparations of first meiotic divisions (see Table 1 for counts and ploidy levels, Fig. 3 for diagrams). a, *Jamesonia Scammanae, Rodman 21a,* × 660; b, *Eriosorus Warscewiczii, Tryon & Tryon 7003,* × 930; c, *E. Warscewiczii* × *Jamesonia Scammanae, Tryon & Tryon, 7048,* × 1060; d, *E. flexuosus* var. *flexuosus, Tryon & Tryon 7014,* × 800; e, *E. glaberrimus, Tryon & Tryon 7061,* × 800; f, *E. flexuosus* × *E. Warscewiczii, Tryon & Tryon 7011,* × 1060; g, *E. congestus, Tryon & Tryon 7044,* × 660; h, *E. cheilanthoides, Plowman 2840,* × 660.

TABLE 1
CHROMOSOME NUMBERS OF ERIOSORUS & JAMESONIA

Species	*Number*	*Ploidy*	*Collection*	*Locality*
Eriosorus congestus (Fig. 2g, 3e)	87^{II}	6×	Tryon & Tryon 6997 (GH)	Costa Rica: Prov. Heredia Vara Blanca
	87^{II}	6×	Tryon & Tryon 7045 (GH)	Prov. San Jose, San Isidro del General
	87^{II}	6×	Tryon & Tryon 7063 (GH)	Prov. San Jose, La Palma
	87^{II}	6×	Tryon & Tryon 7044 (GH)	Prov. Cartago, Empalme
	87^{II}	6×	Tryon & Tryon 7056 (GH)	17 km. S of Cartago
E. cheilanthoides (Fig. 2h, 3f)	174^{II}	12×	Plowman & Sucre 2840/5140 (GH)	Brazil: Rio de Janeiro Mt. Itatiaia
	174^{II}	12×	J. H. Dickson (Manton & Vida 1968)	South Atlantic, Tristan da Cunha
E. flexuous (Fig. 2d, 3d)	87^{II}	6×	Tryon & Tryon 7014 (GH)	Costa Rica: Prov. Alajuela Volcán Poás
	87^{II}	6×	Tryon & Tryon 7016 (GH)	Prov. Alajuela, Volcán Poás
E. glaberrimus (Fig. 2e, 3c)	87^{II}	6×	Tryon & Tryon 7061 (GH)	Costa Rica: Prov. San Jose La Palma
E. myriophyllus	ca. 87^{II}	6×	Tryon & Tyron 6745 (GH)	Brazil: Rio de Janeiro, near Palmares
E. Warscewiczii (Fig. 2b, 3b)	87^{II}	6×	Tryon & Tryon 7003 (GH)	Costa Rica: Prov. Alajuela, Volcán Poás
	87^{II}	6×	Tryon & Tryon 7017 (GH)	Prov. Alajuela, Volcán Poás
	87^{II}	6×	Tryon & Tryon 7050 (GH)	Prov. Cartago, Cerro de la Muerte
E. flexuosus × E. Warscewiczii (Fig. 2f)	ca. 174^{I}		Tryon & Tryon 7011 (GH)	Costa Rica: Prov. Alajuela Volcán Poás
E. Warscewiczii × J. Scammanae (Fig. 2c)	ca. 174^{I}		Tryon & Tryon 7048 (GH)	Costa Rica: Prov. Cartago, Cerro de la Muerte
Jamesonia bogotensis	87^{II}	6×	Tryon & Tryon 6178 (GH)	Colombia: Dept. Cundinamarca, Páramo de Chisaca
J. Scammanae (Fig. 3a, 2a)	87^{II}	6×	Tryon & Tryon 7047 (GH)	Costa Rica: Prov. Cartago, Cerro de la Muerte
	87^{II}	6×	Rodman 21a (GH)	Prov. Cartago, Cerro de la Muerte

Costa Rica suggests that in *Jamesonia,* as well as in *Eriosorus,* species may have stabilized at the hexaploid level.

The hybrids discussed in this work are proposed with confidence in two cases where the putative parents and intermediate

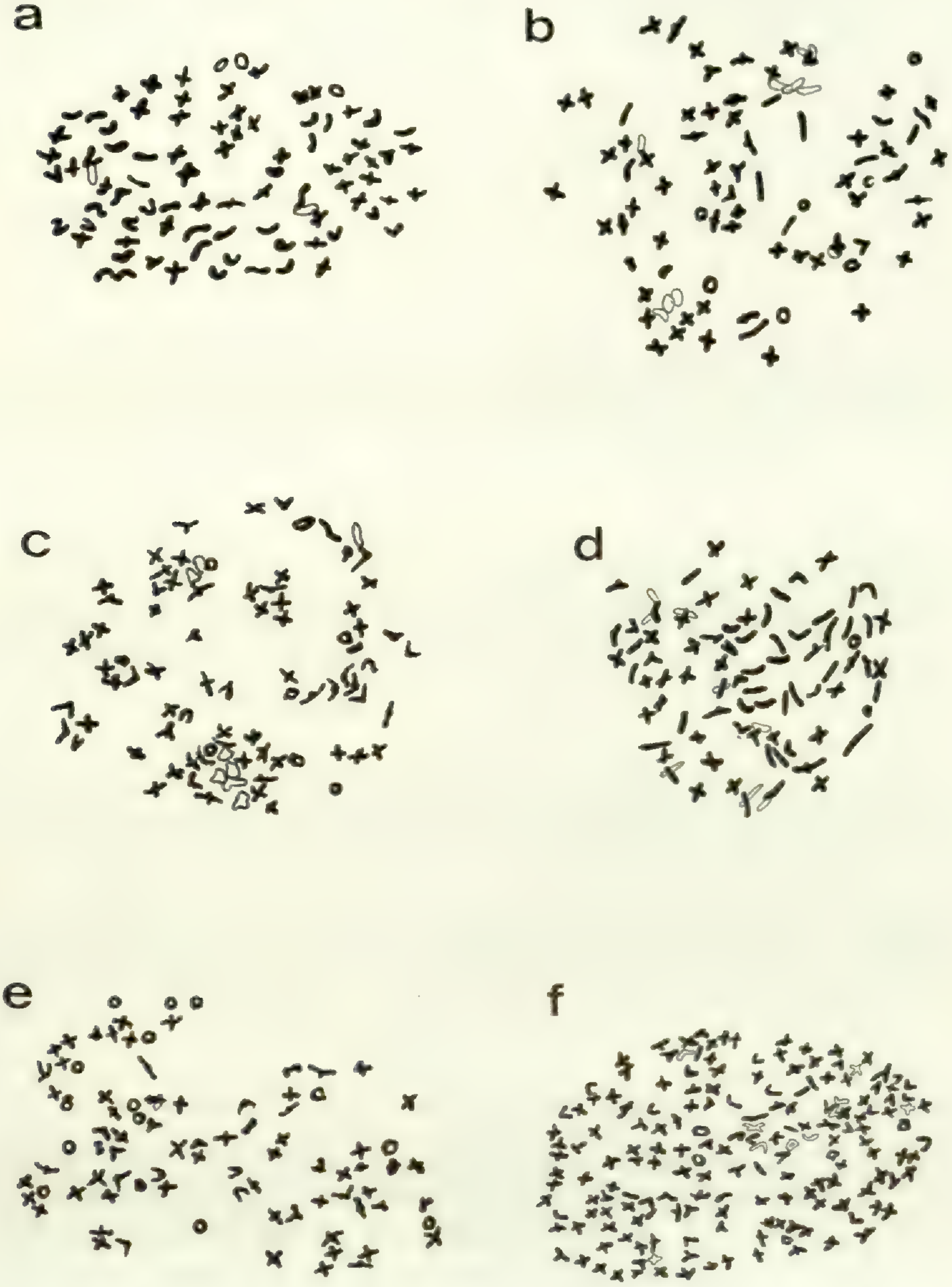


FIG. 3. Explanatory diagrams of species in Fig. 2 showing bivalents in focus in black and the remainder in outline; from the same collections except *Jamesonia.* a, *Jamesonia Scammanae, Tryon & Tryon 7047, n*= 87; b, *Eriosorus Warscewiczii, n*=87; c, *E. glaberrimus, n*=87; d, *E. flexuosus* var. *flexuosus, n*=87; e, *E. congestus, n*=87; f, *E. cheilanthoides, n*=174.

forms are known in the field and have been cytologically examined. Several other putative hybrids are proposed which have not been cytologically studied but are morphological intermediates that can be associated with species occurring in the same habitat or geographic range. Other intermediate collections, noted as variants under the species, are tentatively proposed as hybrids in the hope of providing a useful guide to field work on these complexes. The record of the two hybrids with 174 largely unpaired chromosomes at meiosis, from plants which are morphologically intermediate, indicates that hybridization precedes doubling of the chromosomes. The following observations on the gametophyte and the ecology of the plants are pertinent to hybridization. The gametophytes of *Eriosorus insignis* produced abundant mature antheridia (Fig. 4) prior to archegonia. This sequence is suggestive of an adaptation promoting outcrossing and, under suitable conditions, hybridization. The numerous intermediate forms between species of *Eriosorus* and *Jamesonia* suggest that the integrity of the species in these genera is not so much maintained by genetic incompatibility as it is by the habitat and ecology of the species.

Field observations were made and reported by A. Tryon (1968) on populations in relation to cytological sampling for the Costa Rican species. *Eriosorus congestus* is the widest ranging species of the genus in Costa Rica. There are abundant plants in cut-over pasture land at La Palma and there are also plants of *E. glaberrimus* on the few remaining trees. A collection from this locality was morphologically intermediate between the two species although it resembled the latter more closely in its scandent habit. Unfortunately its sporangia were too mature for cytological study. However, the spores were aborted and on the basis of this, the intermediate morphology of the plant, and the association of the species at this locale, the specimen is considered to be a hybrid of *E. glaberrimus* and *E. congestus*.

On Volcán Poas there are numerous plants of *Eriosorus flexuosus* below the crater and they are especially conspicuous growing among litter remaining after lumbering. This species was also abundant on shrubs nearby in the road clearing with numerous plants of *E. Warscewiczii*. One collection from this site was morphologically intermediate between the two species, although it resembled *E. flexuosus* more closely in its scandent habit. The cytology of this plant clearly showed 174 largely unpaired chromosomes at meiosis.

In the páramo of Cerro de la Muerte, *Eriosorus Warscewiczii* occurs at 3150 m. with *Jamesonia Scammanae* and there are intermediates between these species with ca. 174 largely unpaired chromosomes at meiosis. Similar specimens from Chirripo Grande were described as *Gymnogramma Kupperi*. The reduced, linear leaves of these hybrids resemble those of plants in the Andean *E. cheilanthoides* complex, which also involves *Jamesonia* hybrids. The Costa Rican intermediates and those of the Andes involving *Jamesonia* are difficult to identify without information on the species-association and on the cytology, because the *Jamesonia* characters strongly mask those of the *Eriosorus*.

Gametophytes

There does not appear to be a previous record of gametophytes for the species of *Eriosorus* which are included here. Their spathulate form is uncommon in the *Polypodiaceae* and they are also of special interest because of marked resemblances to the gametophytes of the *Schizaeaceae*.

Spores of three species were germinated in clay pots on sterilized soil with a top dressing of pot chips. The sequence of development was followed for about five months in *Eriosorus insignis* from Brazil *(Tryon & Tryon 6701)* and a shorter time for two other species, *E. hirsutulus* and *E. hispidulus*. The cultures were unfortunately lost by accidental flooding. Several stages in their sequence of growth (see Fig. 4) were traced with the use of a microprojector. The spores of *E. insignis* germinated about fourteen months after they were collected and those of *E. hirsutulus*, collected in 1961, were still viable after five years. In *E. insignis* and *E. hispidulus*, many of the gametophytes form a two-rowed filament by lateral cell division prior to the formation of the thallus plate. In *E. hirsutulus*, the single cell filament persisted more than a month after germination.

In *Eriosorus insignis*, the two-rowed forms are apparent at seven weeks and, as shown in Fig. 4d, they extend to the spore. The apex persists as a single, unusually attenuated papillate cell. There are numerous, coarse, tan rhizoids, often two or more per cell, especially on the lower portion of the filament, a dense mat of which obscures the structure of the lower part of the gametophyte. Thus only a few rhizoids are included in the drawings. Early stages in plate initiation are evident at seven weeks and the spathulate form is well developed by eleven weeks. Series of cells, differ-

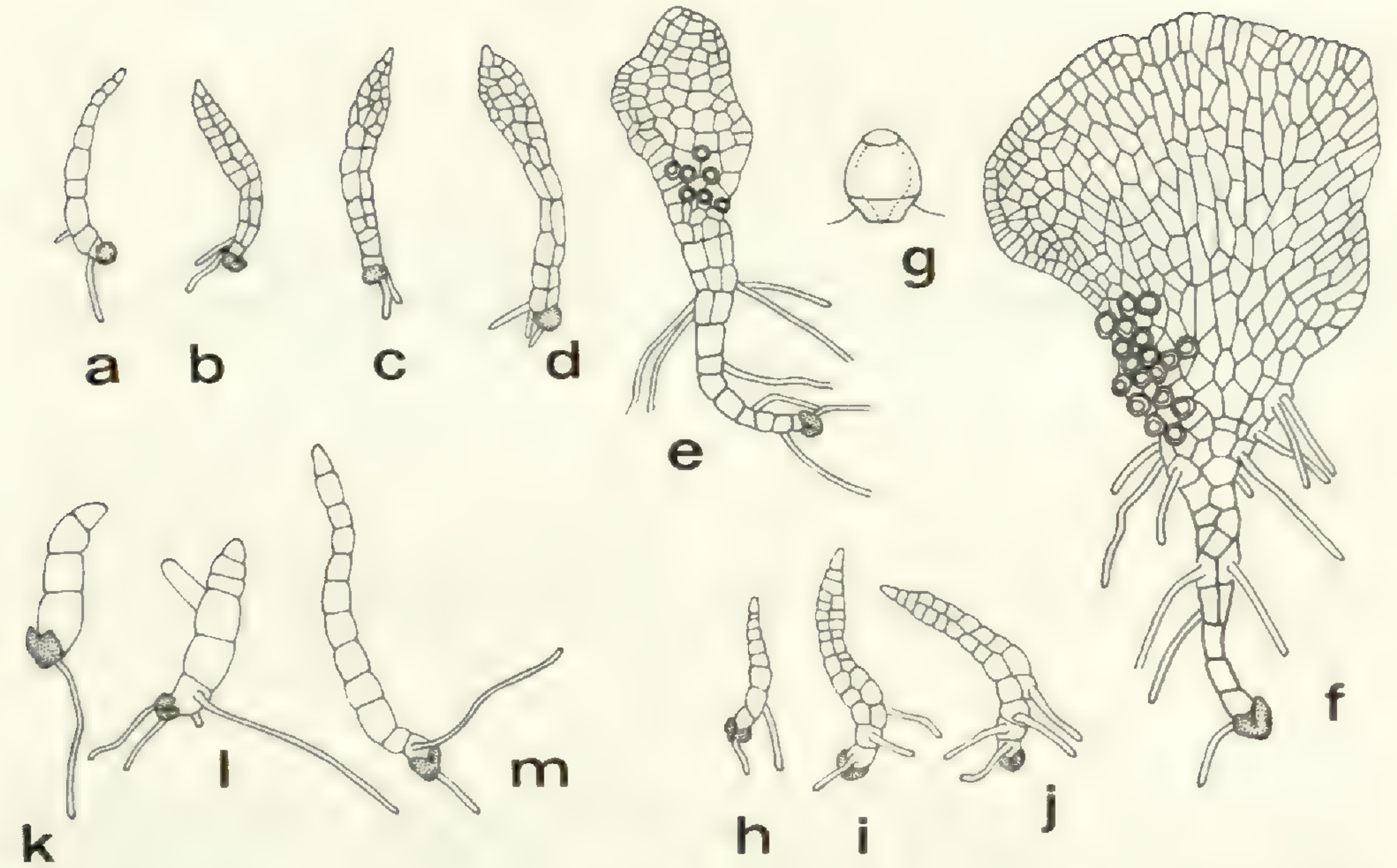


FIG. 4. Gametophytes with some rhizoids and attached spores, a–g, *Eriosorus insignis:* a–d, at seven weeks, e, at eleven weeks with antheridia, f, at five months, with some antheridia and lateral meristem at left, all × 45, g, antheridium, *Tryon & Tryon 6701* (GH); h–j, *E. hispidulus,* at seven weeks, × 45, *Gastony 11* (GH); k–m, *E. hirsutulus,* at eleven weeks, × 60, *Tryon & Tryon 5922* (GH).

entiated from a lateral meristem, are clearly evident by this time and also some antheridia on the lower portion of the thallus. The broad, spathulate form of the gametophyte was maintained in these cultures for a period up to five months. There were abundant, mature and dehiscent antheridia at this time but no archegonia were produced. The three-celled antheridia, shown in Fig. 4g, consist of a short, basal cell below the larger, cylindrical one. The antherozoids are tightly packed and appear to push a funnel-shaped core into the central region of the basal cell. There are few, ca. 20–30, massive antherozoids. The single cap cell of the antheridium dehisces and the antherozoids are released singly through a pore, with the surrounding cell wall forming a spout-like lip. The production of antheridia and absence of archegonia in these gametophytes after five months, suggest that they are adapted to a system of outcrossing. Such a system would be most effective in the formation of the intermediate specimens of plants, regarded as hybrids between species. A discussion of this will be found under several of the species.

Gametophytes of *Eriosorus hispidulus,* Fig. 4h–j, from Puerto Rico *(Gastony 11)* and *E. hirsutulus,* Fig. 4k–m, from Colombia

(Tryon & Tryon 5922) were grown and seemed to develop more slowly but were observed for a shorter time than *E. insignis*, Fig. 4a–g. Their general shape was similar to *E. insignis* but no antheridia were apparent after three months.

An asymmetrical thallus with a persistent lateral meristem is reported for *Anogramma*, and in *Pityrogramma* it later becomes asymmetrical-cordate as reported by Momose (1964). Thus, an affinity between *Eriosorus* and these two genera is suggested by similarities of the gametophyte as well as the sporophyte. The early lateral divisions of the filament, the spathulate shape and lateral meristem in older forms are similar to comparable stages in *Mohria*, and especially in *Anemia*, both of the *Schizaeaceae*, studied by Atkinson (1960, 1962). These similarities are suggestive of broader relationships of *Eriosorus* with that family, and perhaps a closer affinity to it than to genera having wholly cordate gametophytes among the "Gymnogrammoid ferns" in the *Polypodiaceae*.

Morphology and Anatomy

There does not appear to be a comprehensive morphological and anatomical study of this genus. Dunzinger (1901), a student of Goebel, wrote a thesis on the morphology of *Gymnogramma* with many illustrations of the spores. In it, the spores are described for six species which are included here in *Eriosorus*. Bower (1928) included the latter under *Gymnogramma*, which was one of nine genera forming a central group of gymnogrammoid ferns. This group was characterized by stelar systems based upon the solenostele without medullary strands and marked by perforations dividing the leaf into two vascular bundles. The vascular system in the rhizome of *Jamesonia* was described by Bower as a slender solenostele with alternate, elongated leaf gaps and *Jamesonia* was included in a more primitive, primary group of gymnogrammoids.

On the basis of the morphological and anatomical similarities of the rhizome, and on other characters noted in the following discussion, the relationship between *Eriosorus* and *Jamesonia* appears to be a close one. In *Eriosorus* as well as *Jamesonia*, the amphiphloic siphonostele with dictyostelic stages represents an intermediate stelar state between an intact cylinder and a dissected dictyostele with many strands.

A morphological and anatomical survey of all of the species included in this treatment would be too lengthy to present here. However, detailed studies have been made of two of the species which represent distinct morphological forms. They are *Eriosorus myriophyllus* [*Tryon and Tryon 6745* (GH)] collected near Palmares, and *E. cheilanthoides* [*Tryon and Tryon 6724a* (GH)] from Mt. Itatiaia, both in the state of Rio de Janeiro, Brazil. Although these may not be representative of all the species, they may serve as examples for the genus and the following general discussion of morphological and anatomical structures is based mainly on them. *Eriosorus myriophyllus* has a compact rhizome which is larger and less strongly repent than most species. The rhizome in *E. cheilanthoides* is slender, elongate, repent and more characteristic of the genus although the leaves are 2-pinnate and represent a reduced form. Other morphological aspects of the plants such as indument, epidermis, sporangia and spores are more broadly surveyed to include characteristics of these structures which bear on ideas concerning the evolution and phyletic position of the species.

Methods. Specimens were treated according to the techniques outlined by Metcalfe (1960) with modifications as noted. The rhizomes and petioles were boiled and softened in water prior to storage in 70 percent alcohol. Sections were cut between pith on a sledge microtome and cleared in 25 percent hypochlorite solution (Chlorox) for 10-20 minutes. In doing this, the tissue becomes clear and is restored to near fresh condition and requires a shorter time and a less concentrated solution than the treatments outlined by Metcalfe. After being washed and transferred successively to 50 and 70 percent alcohol, the sections were stained in a fresh prepared mixture of one part haematoxylin and 15 parts safranin (1 percent in 70 percent alcohol for 30 minutes). After dehydration in 70, 95 and 100 percent alcohol and transfer to xylol the sections were mounted in Permount. Transverse sections of the pinnae of *Eriosorus cheilanthoides* and of the pinnules of *E. myriophyllus* were prepared by a similar method.

Studies of the epidermis, vascular system of the leaf and segment borders were made from material immersed in 50 percent NaOH from several hours to two days, washed in water, hardened in 50 percent alcohol and then mounted in lactic acid. The diagrams and drawings showing cellular details of structures have

all been drawn from the prepared sections projected on a Bausch and Lomb microprojector. Sporangia and spores were studied mainly from materials mounted in lactic acid, and special preparations are noted in the discussion of spores.

Rhizome. In all species the axis is repent or decumbent. In external morphology, the rhizome is generally cylindrical and elongate, usually with very short, compact internodes. It is slender —less than 10 mm. (usually between 2–4 mm.) in diameter—and sometimes dichotomously branched. The surface is obscured by appressed, bent petioles and adventitious roots which greatly increase the rhizome girth. Anatomical differences in the rhizomes of *Eriosorus myriophyllus* and *E. cheilanthoides* are noted in the description of the tissues. The stelar system is an amphiphloic

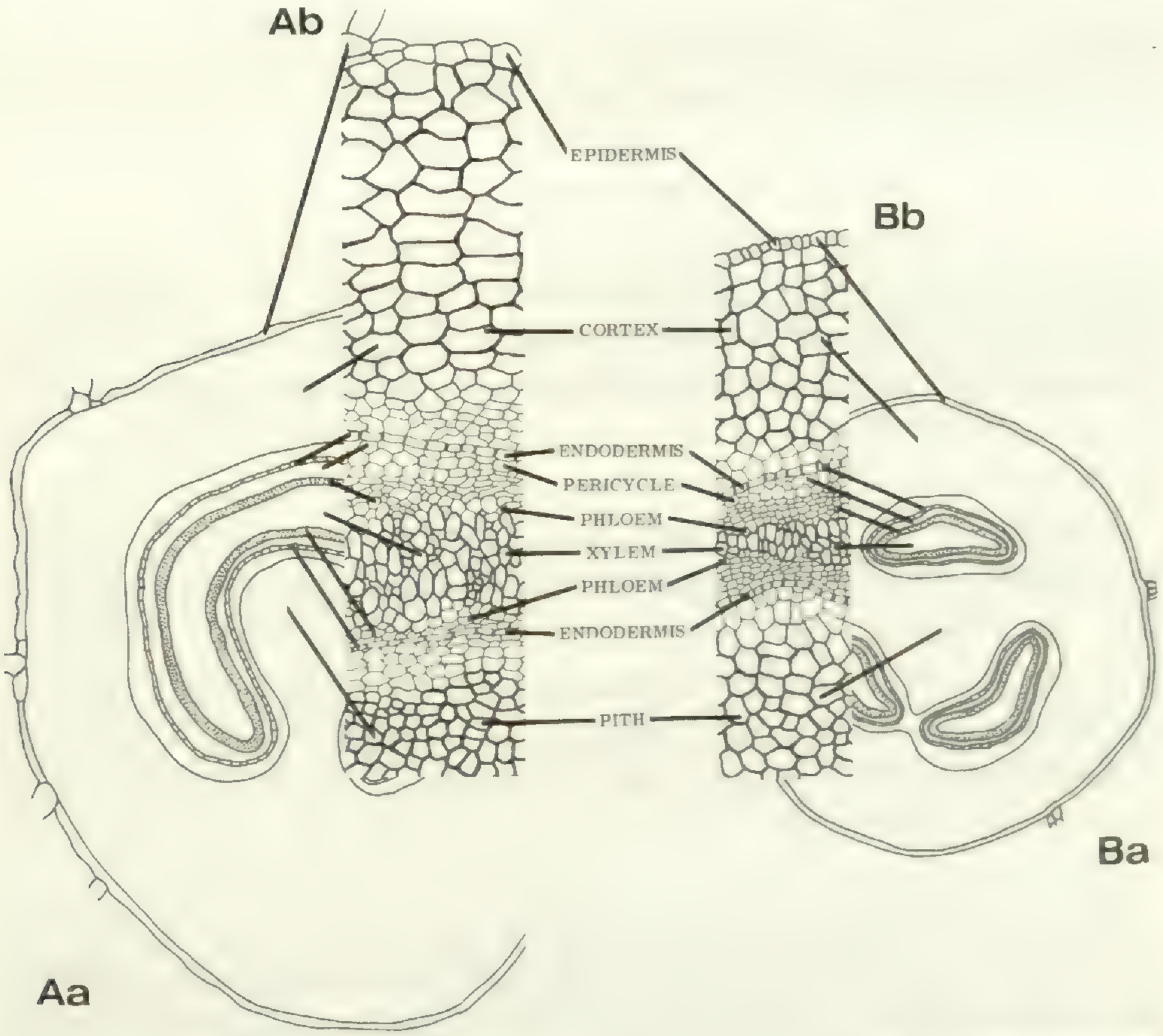


FIG. 5. Rhizome. Diagrams of the amphiphloic siphonosteles and cellular details of tissues traced with the aid of a microprojector. Aa–Ab *Eriosorus myriophyllus:* Aa, diagram with one leaf gap, the epidermis with basal cells of the trichomes; Ab, cellular details, the xylem with parenchyma strands, both from *Tryon & Tryon 6745* (GH). Ba–Bb *E. cheilanthoides:* Ba, diagram with two leaf gaps, near a third, the epidermis with basal cells of the bristles; Bb, cellular details, the xylem of compact tracheids, both from *Tryon & Tryon 6724a* (GH).

siphonostele with an elongated leaf gap usually interrupting the cylinder (Fig. 5Aa) or with two or three overlapping gaps. The slender rhizome in *E. cheilanthoides* has a more complex form with three overlapping gaps (Fig. 5Ba) which approaches a dictyostelic system.

The epidermis is not strongly differentiated from the cortex. In *Eriosorus myriophyllus* (Fig. 5Ab) the cells are more irregularly aligned and thinner walled than in *E. cheilanthoides* (Fig. 5Bb). The basal cells of the rhizome trichomes adjacent to the epidermis are usually larger than those of the epidermis itself. In some sections, cells of both the epidermis and cortex adjacent to the trichomes are enlarged and possibly have a secretory function. Both species have trichomes with glands and *E. myriophyllus* has especially copious exudate.

The cells of the cortex, the pith, and connecting tissue in the area of the leaf gap are strongly lignified. In *Eriosorus myriophyllus* the cells of the peripheral 5–8 layers of the cortex are thicker walled than the central 6–10 layers. In *E. cheilanthoides*, the cortex is composed largely of thick-walled cells comprising 7–10 peripheral layers with 2–4 layers of starch-storing parenchyma cells adjacent to the vascular structure. Thin-walled parenchyma also occurs in the cortex of *Jamesonia* rhizomes but appears to be unusual in other ferns. The lignified cells are especially prominent in *E. cheilanthoides* and constitute the largest part of the cylinder (Fig. 5Bb). The endodermis is readily identified by thin walls and the deep-staining Casparian bands which are most conspicuous, in transverse section, on the radial walls. The endodermis also envelopes the vascular traces connecting with the roots and petioles.

The vascular tissue consists of inner and outer layers of phloem composed of angular, thin-walled sieve and parenchyma cells, surrounding the central xylem core. The most striking difference in rhizome structure between the two species is in the form of the xylem. In *Eriosorus myriophyllus* thin-walled parenchyma cells form conspicuous strands through the xylem, while in *E. cheilanthoides* the xylem is composed wholly of compact lignified tracheids. In both species the tracheid walls have compressed helical thickening.

The indument of the rhizome has been employed in several classifications and phyletic schemes treating the "Gymnogram-

moids," including *Eriosorus*. Simple rhizome trichomes are one of the basic characteristics unifying the central genera of the "Gymnogrammoides" and also of the larger group, "Chaetopterids," of the *Polypodiaceae*. Structure of the rhizome indument has been studied here in some detail because of its taxonomic importance. In the descriptions of the trichomes, differences in the disposition and color are noted and also the number of basal cells and the shape of the apical cell. Unfortunately, many of the collections are without rhizomes. They are not known in *Eriosorus Orbignyanus* and *E. accrescens*, and in *E. Ewanii* only rhizomes of juvenile plants have been seen.

The general form of the rhizome indument in *Eriosorus* ranges from a simple, uniseriate trichome to a broad, flattened true scale. Uniseriate trichomes occur adjacent to the rhizome apex in all species, and this is considered to be a basic form characteristic of the genus. Rhizome indument in 17 species is predominantly of this type, but in several species the indument is essentially trichome-like but with two to four cells at the base. These rather simple bristles represent forms intermediate between trichomes and thickened, broad bristles. In six species, some of the indument is broader at or near the base, up to 10 cells wide, several cells thick, and is deep brown to black in color. These structures are also regarded as bristles but represent scale-like forms. The exceptional occurrence of true scales in *E. flexuosus* var. *galeanus* (Fig. 33Ba) clearly represents a specialized type of indument. The rhizomes of var. *galeanus* have bristles as well as light brown or tan colored, flattened scales.

The rhizome trichomes are often glandular with the apical cell inflated—usually pyriform or capitate. The wall of the apical cell is much thinner than other cells of the trichome and the outer layers appear to be lost as the cell becomes secretory. In the descriptions of the species, trichomes are noted as glandular when exudate is apparent on the apical cell.

The occurrence of bristles and scales in *Eriosorus* correlates with other more specialized morphological characters. Most species with such indument also have elaborated, scandent, or reduced linear leaves and some also have more specialized spore characters. These correlations, as well as the occurrence of simple trichomes in all of the species, reinforce the concept that bristles and scales represent a derived state in the genus.

Roots. Adventitious roots are found on all surfaces of the rhizomes. They are usually more abundant adjacent to the petioles than elsewhere, but often densely clothe the entire structure. In *Eriosorus myriophyllus* they are deep brown, strongly bent, widely spreading and usually about 1 mm. in diameter. In *E. cheilanthoides* they form a compacted mat around the rhizome, are light brown, less than 0.5 mm. in diameter, and are densely covered with lustrous, gold-colored root hairs. A collar of epidermal tissue protrudes from the rhizome surface and ensheaths the roots. This structure, illustrated in *E. insignis* (Fig. 6a) is characteristic of the adventitious roots in both *Eriosorus* and *Jamesonia*. The epidermis, in transverse section, consists of thin-walled cells, smaller than those in adjacent cortical tissue. Cortex cells in the outer 4 or 5 layers have slightly thicker walls than the epidermis and contain deep-staining inclusions. An inner layer adjacent to the

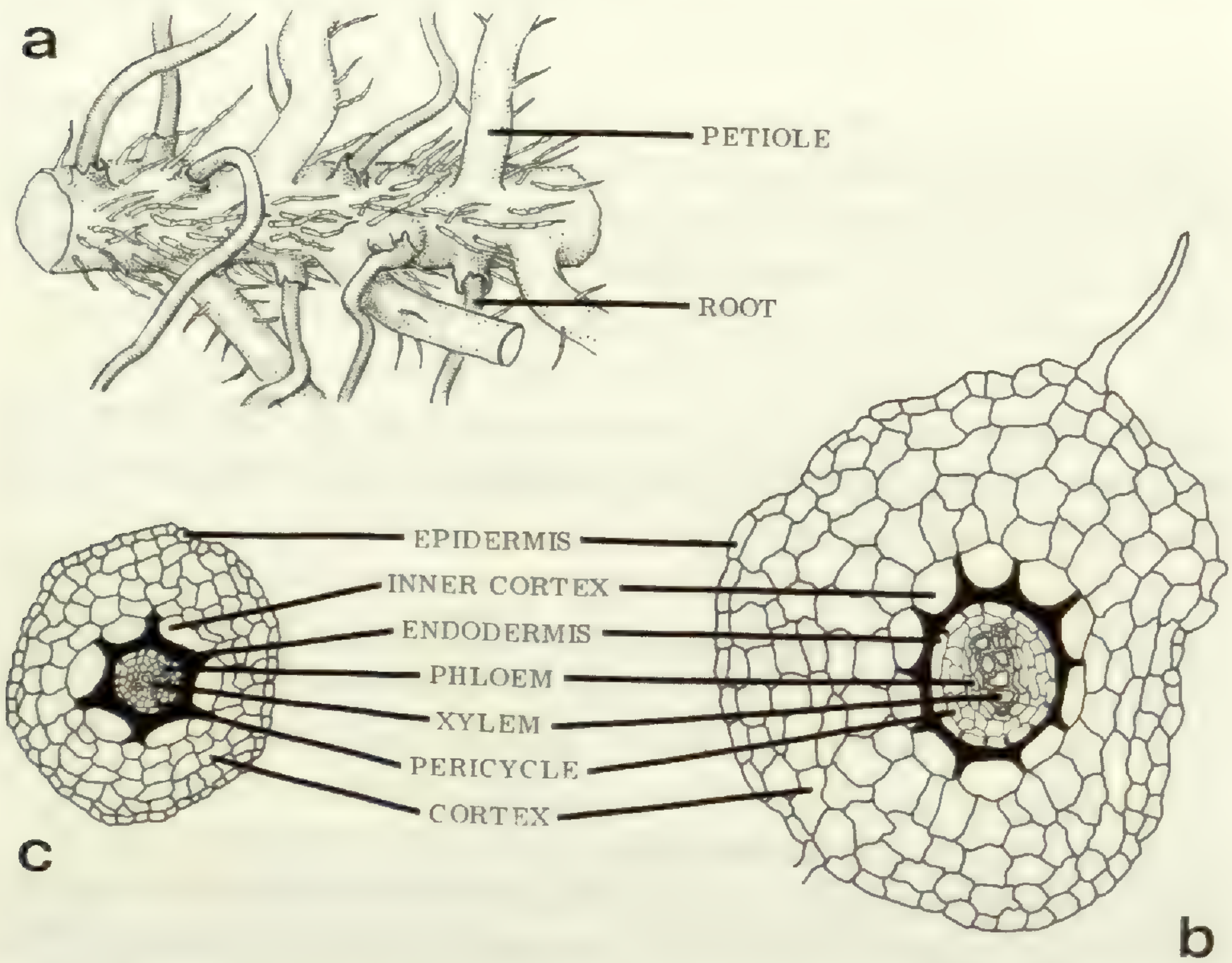


FIG. 6. Root: a, Portion of rhizome with five petiole bases, adventitious roots with ensheathing collars, and trichomes, enlarged, *Eriosorus insignis, Brade 15802* (RB); b, c, transverse sections of root with thickened inner cortical layer in cellular detail, traced using a microprojector; b, *E. myriophyllus, Tryon & Tryon 6745* (GH); c, *E. cheilanthoides, Tryon &Tryon 6724a* (GH).

endodermis (Fig. 6c, b) has very large cells with differential thickening on the inner tangential and radial walls. The endodermis is composed of a relatively few elongate cells with conspicuous Casparian thickening on the radial walls. The vascular tissue consists of a central xylem core of 4–6 large tracheids with groups of smaller protoxylem elements at opposite ends, in a diarch arrangement. Elongated phloem cells with angular walls are clustered, adjacent to the larger tracheids. The pericycle consists of 1–3 layers of larger parenchyma cells, which are between the phloem and endodermis.

The peculiar, enlarged cells with thickened walls in the inner cortex of *Eriosorus* (Fig. 6b, c) are located in a position similar to a layer of enlarged but unthickened cells in the roots of *Adiantum*, as described by Ogura (1938). In the roots of *Anemia colimensis*, similar tissue is described by Mickel (1967) as "a sclerified palisade layer of inner cortical cells." The differential deposition confined to the radial and inner tangential walls of this tissue in *Eriosorus* resembles the endodermal thickening reported by Esau (1953) in roots of certain monocots.

Leaves. The leaves are closely placed on the rhizome in most species. They are borne in a spiral sequence but with paired members in nearly opposite positions on the stem. The leaves show greater variation than other organs and in this genus there are major trends toward reduction and elaboration of the lamina. A tendency toward leaf dimorphism is apparent in several species but is most pronounced in *Eriosorus hispidulus*.

Leaf complexity is quite variable. In the descriptions of the lamina, division is given in respect to the "normal" maximum, exclusive of exceptional cases of further division. Representative portions of leaves are shown in Fig. 7 to illustrate the use of the terms lobe and ultimate segment as applied in the descriptions. The term ultimate segment is especially critical in *Eriosorus* and it is applied to the ultimate division of the lamina having two or more veins. It is used with reference to leaves with segments of tertiary or a higher order (the primary order is equivalent to the pinna and the secondary to the pinnule). Definitions of other terms follow those in the glossary of terminology of the fern leaf by Rolla Tryon (1960). The term pinnatifid is not used here as it cannot be applied consistently in this genus with any precision.

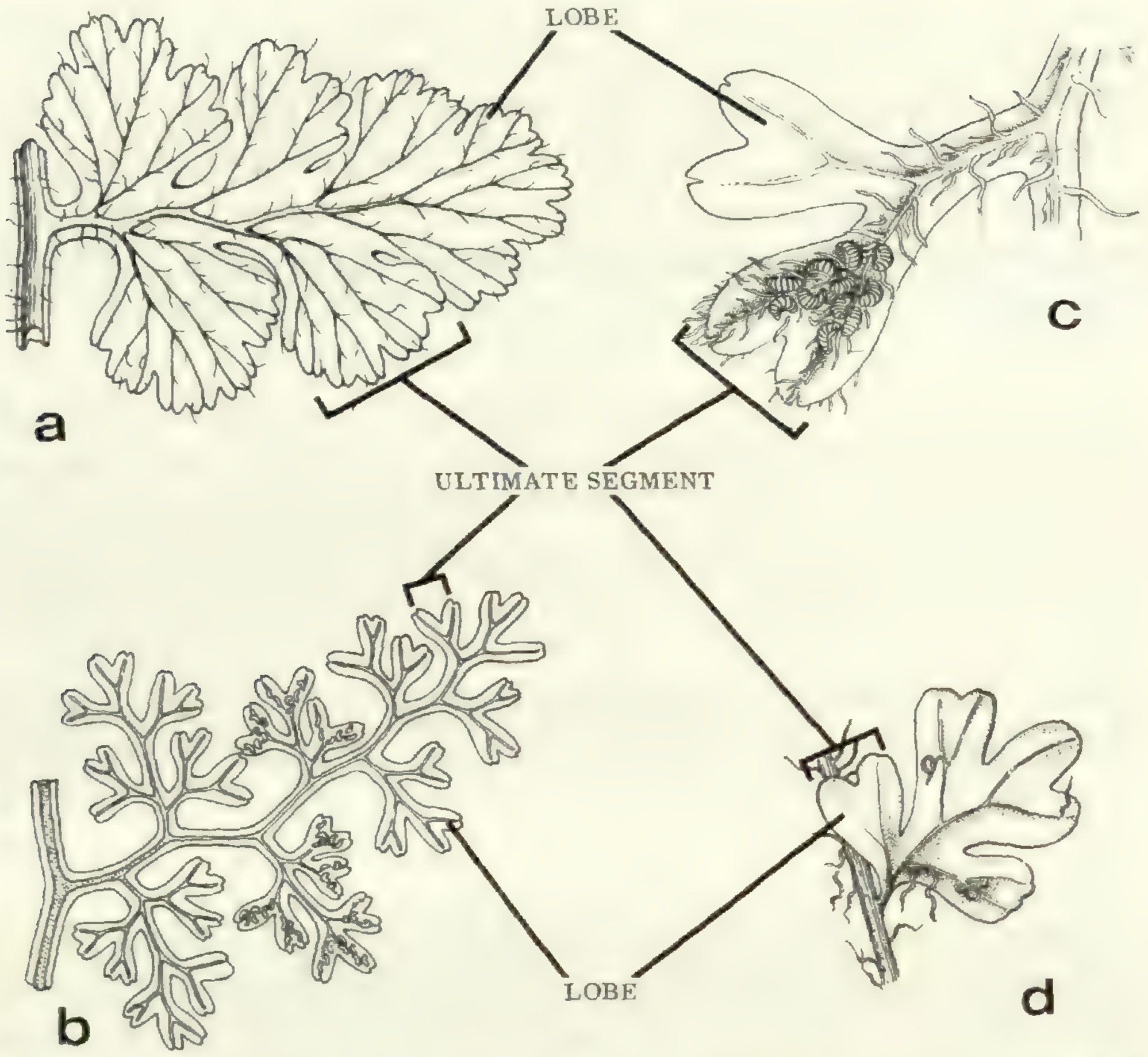


FIG. 7. Leaf complexity with terms applied in descriptions. a, pinnule, secondary division of 3-pinnate lamina; b, tertiary segment of 6-pinnate lamina; c, two ultimate segments; d, pinna, primary division of 2-pinnate lamina.

The least complex lamina, in *E. longipetiolatus*, is about 10 cm. long, once pinnate and with as few as 13 entire pinnae. In the most complex leaves, as those of *E. flexuosus*, the lamina may exceed four meters in length, is scandent or scrambling, fractiflex and up to six times pinnate with the pinnae oriented in several planes. Leaves of both of these species represent extreme forms. Most species have the lamina 30–50 cm. long and are two or three pinnate.

Epidermal cells of the leaves, in transverse section, are oval or have irregular lobes protruding into the adjacent spongy tissue. The cells of the lower epidermis are slightly smaller and have stomates which do not, or only slightly, protrude from the surface. Cell wall patterns of the leaf epidermis are included in the figures for each species. They were traced, using a microprojector, from segments partially cleared in sodium hydroxide. The tissues were

peeled, mounted in lactic acid and the cell walls were traced from comparable regions between the veins. Cells of the lower surface, adjacent to the veins, are usually longer than those between the veins. Several examples of variant patterns are illustrated from samples of *Eriosorus flexuosus* and *E. hirtus* showing the differences in size, density and orientation of the guard cells. *Eriosorus* was not included in the survey of stomates in the ferns by Kondo (1962), but the pattern resembles that of *Woodwardia orientalis* and is of the 2A type in his system. This type is based on the development of the guard cells and their attachment to the cell walls after division of the stomatal initial.

Among epidermal cell wall patterns of *Eriosorus flexuosus* (Fig. 34) the smallest guard cells (Fig. 34Ab) are found in the type collected in the vicinity of Caracas. In contrast, the largest cells (Fig. 34Ah) are found in the hybrid with *E. paucifolius* from Cerro Auyantepui in southern Venezuela. The patterns in *E. flexuosus* from Mexico (Fig. 34B) have exceptionally undulate walls in the upper epidermis and the guard cells are only slightly smaller than those of the hybrid. The collection from Cerro Auyantepui is treated as a hybrid on the basis of an intermediate leaf form between that of *E. flexuosus* and *E. paucifolius*. The spores are unusually sculptured with exceptionally broad, irregular equatorial flanges. The large epidermal cells in these specimens may also indicate a hybrid origin of these plants. Such differences in the epidermal cells and spores when correlated with chromosome numbers may allow a preliminary assessment of polyploidy from herbarium specimens.

The leaf rachis usually has a slightly lighter color than the petiole and in *Eriosorus myriophyllus* and *E. flexuosus* it is mostly straw colored or tan. The channel on the adaxial surface is continuous with that of the pinnae stalks. The lamina tissue is often decurrent on the rachis, especially in the apical portion of the leaf. A single vascular strand extends throughout the rachis and in transverse section the tissues are similar to those in the petiole apex.

The lamina is anadromic in leaves more than once pinnate and the basiscopic pinnules, especially in the basal pinnae, are usually enlarged. These characteristics of the lamina are useful in reconstructing the position and orientation of fragmentary portions of large leaves.

The petiole bases are usually appressed to the rhizomes and are strongly bent or bowed. This orientation of the petioles is similar to that in *Jamesonia* and some species of *Pterozonium.* They are more strongly appressed to the rhizome than in other groups, such as *Pellaea,* which also have slender, elongate rhizomes. The petiole length may vary from 1/12 as long as the lamina, as in *Eriosorus cheilanthoides,* up to four times longer than the lamina as is found in the aptly named *E. longipetiolatus.* Near the rhizome the shape is terete or subterete and at the apex it is plane or channeled on the adaxial surface. The color is usually brown ranging from castaneous to atropurpureous except in *E. myriophyllus* and *E. flexuosus,* in which the apex is usually tan.

In transverse section, the epidermal cell walls appear strongly thickened and the lumen is small and irregular. The cortical cell layers nearest the epidermis also have thickened walls but the lumen outlines are fairly regular. The largest portion of the cortex, 7–12 layers outside of the endodermis, is made up of thin-walled parenchyma. The vascular tissues near the rhizome form a broad U-shaped strap, becoming sharper and V-shaped near the apex of the petiole. Protoxylem occurs at the base of the V and at the ends of the arms where it is overarched by a few metaxylem cells. In *Eriosorus myriophyllus* the xylem has strands of parenchyma similar to those found in the rhizome of this species. The phloem is mainly along the outer sides of the arms and interrupted or with few cells at the ends.

Veins. Veins usually terminate at the margin of the ultimate segments. In *Eriosorus Lindigii, E. hirsutulus* and *E. hispidulus* the veins terminate short of the margins. This condition is so constant that it is useful in characterizing these species. The vein ends are usually only slightly broadened in most species but in *E. rufescens* and the closely allied *E. setulosus* they are much enlarged to broadly clavate or cuneate. The vein ends are quite elaborate in *E. Stuebelii* and *E. aureonitens.* They are not only enlarged but, in the latter especially, the veins protrude into the teeth along the segment margins. In *E. longipetiolatus* the veins are deeply immersed in the coriaceous lamina tissue. In *E. Biardii,* which has an herbaceous lamina, only the ends are immersed on the abaxial surface. The most extreme elaboration of veins is found in *E. Ewanii* where the ends are strongly dilated into a pad of thickened tissue. This is particularly remarkable as it shows the development of a completely unique character in the genus.

The trichomes of the lamina, particularly among the sporangia, were compared in *Eriosorus*, *Jamesonia* and *Pterozonium* by A. Tryon (1965) with respect to the definition of paraphyses. Names of some taxa used in that work have been changed and terms have been clarified in this revision, but the following basic idea is re-emphasized. In *Eriosorus* the indument occurring among the sporangia consists of trichomes; they may be glandular, but are not differentiated from those on other parts of the lamina, and cannot be construed as being paraphyses.

Leaf trichomes which are described as crispate may be variously curled or twisted and are disposed in a lax manner. These contrast with rigid ones which are usually shorter and erect or appressed. The elongate apical cell of the trichome is usually somewhat acuminate and tapers to a rather rounded apex. The form of the globose apical cell ranges from slightly enlarged to pyriform or capitate. The trichomes may be clear and quite colorless, tan to deep brown, or bicolorous. More than one form of trichome may occur on the same structure, as is often the case on the rachis and petiole. A few species seem to have essentially glabrous mature leaves, but some type of indument usually occurs in channels on the adaxial surface of the rachis and also at the pinnae axils. In *Eriosorus Wurdackii* the adaxial leaf surface appears glabrous but there are tufts of deep brown trichomes at the pinnae axils which are similar to trichomes at the axils in *Pterozonium*.

The petioles often appear less strongly indumented than other parts of the leaves, but there are usually many scars from deciduous indument on the epidermis. Petiolar indument is complex because near the base it resembles the rhizome indument. It is usually more abundant at the apex and there it resembles indument of the rachis.

The greatest development of leaf indument in *Eriosorus* is in *E. aureonitens* and *E. Stuebelii* the Andean species occurring from southern Colombia to southern Peru. The leaves of these species are completely enveloped in tawny or rust colored tomentum similar to that found in several species allied to *Jamesonia canescens* which grow in northern Colombia and Venezuela. There are no close geographical connections between these groups and there are no other resemblances; thus, it seems there has been a parallel development of the tomentose condition in the two genera. This type of indument contrasts with that in *E. rufescens*, *E. setulosus* and *E. longipetiolatus* in which the trichomes are

discrete, rigid and usually bicolorous, ruddy or deep brown and clear or tan at the base. These rigid trichomes are similar to those in *Jamesonia cinnamomea* and *J. Goudotii* which occur on the same páramos in southern Colombia with these *Eriosorus* species. The similarity of indument and their close geographical associations suggest possible hybridization as noted in the discussions of *E. setulosus* and *E. longipetiolatus*.

About half of the species of *Eriosorus* have trichomes bearing copious exudate on the apical cells. There are different forms of the glands. In *E. myriophyllus* they have a pyriform apex borne on a long, uniseriate stalk and are quite distinct from the glands with a capitate apex on a short stalk, as in *E. Ewanii*. In the latter species, the leaf surfaces are densely covered with capitate glands also characteristic of *Jamesonia cinnamomea*, which occurs on the same páramos in southern Colombia with *E. Ewanii*. The similarity of indument and geographic associations of these plants suggests the possibility of hybridization involving *Jamesonia* as noted in the discussion under *E. Ewanii*.

Sporangia. The sorus in *Eriosorus* usually extends for most of the length of the veins in the ultimate segments and there is no indusium. The sporangia develop in an outward (or acropetal) sequence progressively along the vein toward the margin. The developmental sequence of the sporangia differs from that in other genera such as *Pellaea* and *Notholaena* in which the younger sporangia are produced basally on the veins. In other "Gymnogrammoid" genera with prolonged linear sori, such as *Syngramma, Craspedodictyum* and *Aspleniopsis*, the sporangia are in a mixed state of development along the veins and the youngest are not concentrated in the distal portion as they are in *Eriosorus*. The mature sporangia are often most abundant on the penultimate veins. In *E. Wurdackii* and *E. Orbignyanus* they are restricted to the terminal portion of the veins and form submarginal bands.

Sporangial structure of *Eriosorus congestus* (see Fig. 8) shows differences in the two faces, especially the marked asymmetry of the capsule. The form is generally pyriform and somewhat longer than broad, or orbicular. The annulus is interrupted by the stalk and the number of indurated cells ranges from 12–26. The number of annular cells was formerly considered to be, but is not, taxonomically significant in this group. There are 2–6 thin-walled cells between the annulus and stomium and below these 2–4

indurated cells, between which the sporangium opens. There is usually a tier of three cells directly subtending the capsule and from 1–3 tiers between this and the receptacle. The sporangia in *Eriosorus* differ from those of other groups in the *Polypodiaceae* which have elongated stalks. The lower cells of the stalk in *Eriosorus* may increase by intercalary division and form a cushion of cells which is not readily distinguishable from cells of the receptacle. In *E. velleus,* five capsules may be subtended by a single cushion of cells. In *E. rufescens, E. hirsutulus* and *E. cheilanthoides* there are often trichomes on the stalk or cushion similar to those on other parts of the leaf. The form of the stalk (Fig. 8a) with three cells adjacent to the capsule and one or two unthickened tiers adjacent to the receptacle is more frequent in the genus and regarded as the more generalized type of sporangium than that with intercalary divisions as noted above.

Spores. Remarkably good descriptions and illustrations of spores were done by Dunzinger (1901). In his treatment of *Gymnogramma,* he regarded spores as the most useful character for establishing species groups. The illustrations, although simple line drawings, clearly show the unique sculpture of the spores in lateral view as well as on the main faces. Irregular or aborted

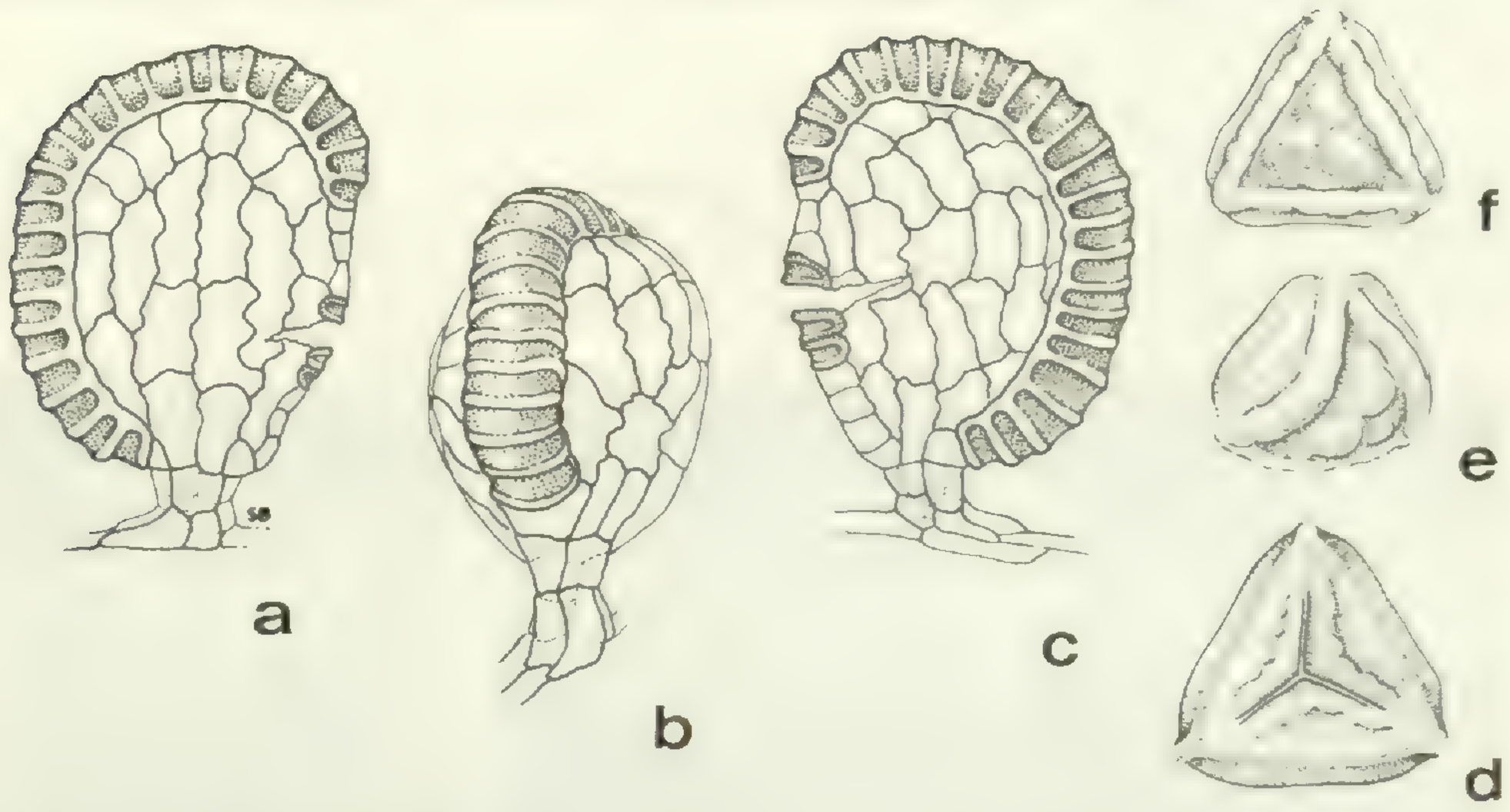


FIG. 8. Sporangia and spores. a–c, Sporangia, × 85, *Eriosorus congestus:* a, proximal face, the stalk with three cells subtending the capsule; b, lateral view showing excentric annulus; c, distal face, *Tryon & Tryon 7018* (GH). d–f, spores, *E. flexuosus:* d, proximal face with equatorial flange at the perimeter with three projecting angles; e, lateral view with two ridges of distal face intersecting in an angle near the equatorial flange; f, distal face with three ridges forming basal triangle and tubercles within the central areola, *Tryon & Tryon 7010* (GH).

spores were noted in *Gymnogramma elongata*. They obviously represent spores of one of the hybrids which are frequent in this complex, treated here under *E. cheilanthoides*. In the survey of spores by Erdtman (1957) *Gymnogramma (Eriosorus) congesta* is illustrated, including the surface detail on the two faces. Fragments are shown which infer that a layer exists outside of the exine in these spores. *Eriosorus flexuosus* spores are illustrated by Tschudy and Tschudy (1965) and they indicate that these spores are without perine. My observations confirm this and I consider the fragments of perine shown by Erdtman to be related to the deteriorated wall resulting from acetolysis.

Spores of all of the species were examined in dried condition and in lactic acid preparations. Several species were also studied from preparations cleared by acetolysis or by sodium hydroxide. These cleared materials were useful for examination of some of the surface detail but the spores became decolorized and were disintegrated in the process of acetolysis. Deterioration of preparations by the same process was also reported by Tschudy and Tschudy and they attribute this to a chemical breakdown of the cell wall. Spores of *Eriosorus hirtus* and *E. congestus* were examined with a scanning electron microscope (Fig. 9a-c). The following general descriptions were drawn from both light and scanning microscope studies.

There are usually 64 spores per sporangium and this is considered to be the normal complement. There is considerable variation

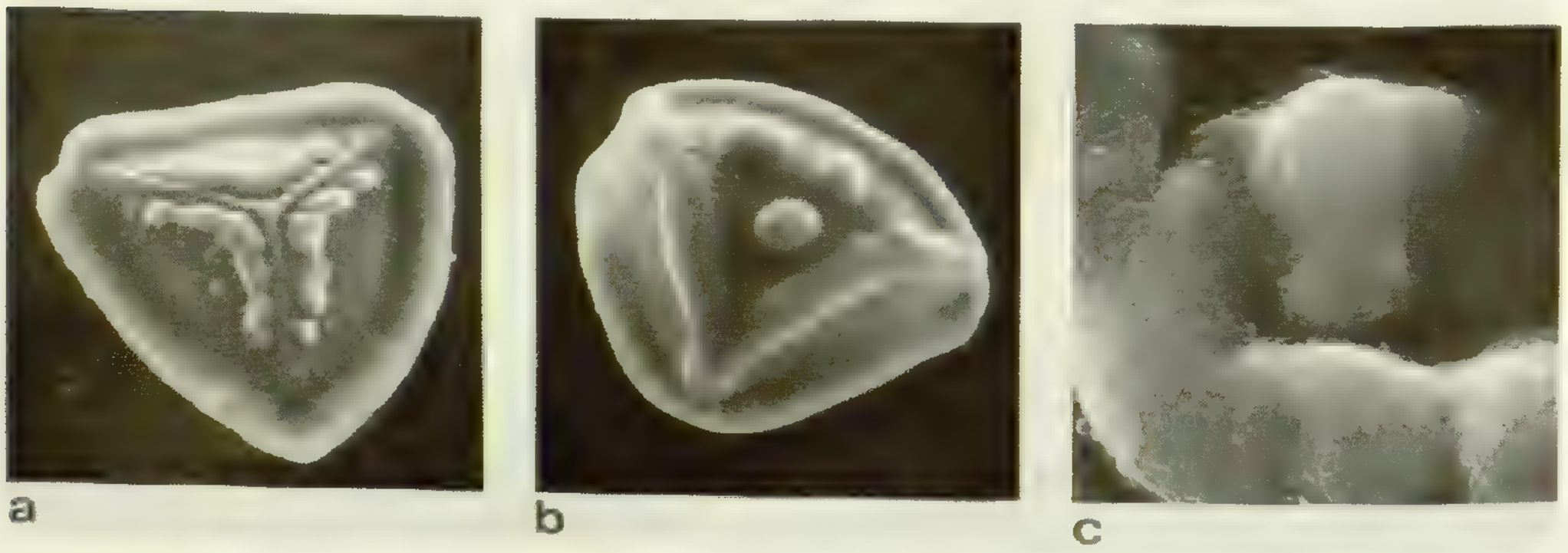


FIG. 9. Photographs of spore details from scanning electron microscope studies: a, Proximal face with central triradiate scar, adjacent tubercles and equatorial flange in perimeter; b, distal face in oblique view with two basal ridges intersecting and three tubercles within central areola, both *Eriosorus congestus, Tryon & Tryon 6995*, × 500; c, surface detail of ridges and floor of proximal face, *E. hirtus, Williams & Alston 294*, × 2660.

in size. The spores examined, which were mounted in lactic acid, showed the greatest diameter of the polar face from 40–80μ. There seem to be correlations between spore and epidermal cell size which may be of interest in the analyses of hybridization and polyploidy in the species. A good indication of hybridization or some other irregularity in specimens is poorly developed or aborted spores, but this is not wholly reliable. There are some specimens which have abundant well-formed spores that seem to be hybrids on the basis of other morphological characters. A study of the spores of such variants, using the scanning microscope, showed irregularities in the structure of the equatorial flanges although the spores appeared well-formed.

Spore color in *Eriosorus* is usually brown, ranging from a moderately dark, ruddy shade to deep brown. Among four species with light brown or tan spores, *E. hirtus* and *E. hispidulus* are closely related and represent derived forms in other aspects and *E. flexuosus* and *E. cheilanthoides* are quite distantly related but represent specialized forms in the genus.

Spore shape is basically tetrahedral but flattened on three meridional planes which are compressed by contact in the tetrad. The free convex surface is slightly larger than a half sphere and elongated in lateral view. The proximal face (Fig. 8d) is subtriangular in outline with three convex sides and three angles more or less protruding from the flange or subtending ridge. The triradiate scars are slightly raised and extend ½–¾ the distance to the equator. There are broad, parallel ridges or projections, variously coalescent, which form the margo. The ridges, highly magnified in Fig. 9c, consist of coarse, pebbled material. The exine texture of both sculpture and floor appears to be uniform over the entire spore surface. The equatorial ridge is noted in the descriptions as a flange. This may be variable in width and quite thick, and is more or less extended at the three angles which are aligned with the triradiate scar. On the distal face (Fig. 8f) three contiguous ridges form a triangular base upon which the spore usually rests. The spores are usually oriented with the proximal or polar face upright. This orientation is possibly advantageous for germination of the spores or early growth of the gametophyte. The central areola within the basal triangle may be quite smooth, papillate or often includes several coarse tubercles. The angles of the basal triangle are connected by short ridges which extend up to and

often protrude slightly at the equatorial flange. In *E. myriophyllus* and *E. Sellowianus* the triangle is large. The ridges of the triangle are up on the lateral spore surfaces, nearly parallel to the equatorial flange, and their ends protrude at the three angles.

The spores of *Eriosorus* are similar to those of *Jamesonia* and are characteristic of these genera. They are similar to *Anemia* spores in that the three angles prominently protrude at the equator and that they possess strong, coarse ridges. The variant pattern of parallel ridges noted above in *E. myriophyllus* also resembles the prominent banding in the equatorial region in spores of *Anemia*. This also suggests a possible origin of the characteristic basal triangle in *Eriosorus* spores from more contiguous ridges in the equatorial region.

SYSTEMATIC TREATMENT

Eriosorus Fée, Genera Filicum 152, t. 13B, f. 1. 1852. Copel. Gen. Fil. 58. 1947. TYPE: *Eriosorus scandens* Fée=*E. aureonitens* (Hook.) Copel.

Psilogramme Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 332. 1882. TYPE: *Gymnogramma elongata* Hook. & Grev.=*Eriosorus cheilanthoides* × *Jamesonia*.

Psilogramme, Section *Eupsilogramme* Kuhn, op. cit. 335. 1882.

Gymnogramma auct., non Desv. Mag. Ges. Naturf. Berlin **5**:304. 1811, id est C. Chr. in Verdoorn, Man. Pterid. 304. 1938: Reimers, in Engler, Syllabus Pflanzfam. ed. 12, **1**:302. 1954.

Rhizome repent, usually with short, compact internodes, an amphiphloic siphonostele with dictyostelic stages, densely clothed with golden brown to black, rigid or crispate, erect or appressed trichomes or bristles, with 1–10 cells at the base, rarely scales. *Leaves* usually erect, sometimes scrambling or scandent. *Lamina* elongate-triangular, -rhomboid or linear and 30–50 cm. long, not exceeding 20 cm. and usually less than 10 cm. wide, 1-pinnate to usually 2–3-pinnate, or scandent and up to 4 m. long, 50 cm. wide and 6-pinnate. *Petiole* terete or subterete, near the apex usually plane or channeled on the adaxial surface, this and the rachis atropurpureous or castaneous, rarely tan, usually pubescent or glandular, the rachis sometimes fractiflex. *Pinnae* usually ascending, sometimes descending, from the rachis, usually elongate-triangular or -ovate, usually herbaceous, sometimes coriaceous, more or less pubescent or glandular, especially on the abaxial surface, sometimes tomentose, the *ultimate segments* or lobes usually bifid, or orbicular or ovate; *veins* free, dichotomous, usually extending to the margin or sometimes short of it, the ends more or less enlarged to clavate; *border* usually with 1–3 rows of elongate cells, sometimes irregularly dentate or papillate, especially at the segment apex, or sometimes with trichomes. *Sporangia* along the veins, most abundant on the penultimate and at base of ultimate veins, sometimes restricted to a portion of the vein and aligned in a submarginal band, developing in acropetal sequence, the capsule usually pyriform or orbicular, the annulus of 12–26 indurated cells, the stalk of 2 or 3 tiers

subtending the capsule, often with intercalary cell divisions forming a cushion of cells adjacent to the receptacle, sometimes with trichomes on the stalk. *Spores* tetrahedral, deep to ruddy brown or lighter, sometimes tan, the proximal face with prominent ridges or tubercules adjacent to the triradiate scar, with a moderate to broad equatorial flange, the three angles confluent with the scars more or less protruding, the distal face with three ridges forming a basal triangle, these sometimes near the equatorial flange on the lateral spore surfaces, the areola within the basal triangle smooth or more or less tuberculate. Gametophyte spathulate with a lateral meristem.

KEY TO THE SPECIES OF ERIOSORUS

a. Leaves scandent, twining or scrambling, up to 3 meters long (specimens usually incomplete), 4 or more times pinnate. b.
b. Ultimate segments dichotomously lobed to deeply bifid, slender, usually with 1 or 2 veins. c.
c. Vein ends not enlarged to somewhat clavate; lamina glabrous or sparsely pubescent, rarely with glandular trichomes. d.
d. Rachis castaneous or deep brown throughout; pinnule rachises arcuate, descending from the pinna rachis in an arc or angle greater than 90 degrees; lamina glabrous; spores deep brown .... 25. *E. glaberrimus.*
d. Rachis castaneous or deep brown below, the upper portion, especially near the apex, tan or straw colored; pinnule rachises fractiflex, usually ascending at an angle with pinna rachis of less than 90 degrees; lamina more or less pubescent; rarely glandular; spores tan or light brown ..... 22. *E. flexuosus.*
c. Vein ends enlarged, usually dilated at the end, forming a pad of thickened tissue at the margin; lamina hispid, with rigid, glandular trichomes ..... 23. *E. Ewanii.*
b. Ultimate segments orbicular or cuneate (not dichotomously lobed), broad with 6 to 20 or more veins ..... 20. *E. Orbignyanus.*
a. Leaves erect or if scandent or scrambling 1 to 3 times pinnate; lamina of mature leaves mostly between 5–50 cm. long, usually not exceeding 70 cm. e.
e. Leaves linear, usually 1- or 2-pinnate, the pinnae about as long as broad (rarely in intermediates, up to 4 times longer than broad). f.
f. Lamina usually with patent, clear or concolorous trichomes or glands; pinnae herbaceous to chartaceous. g.
g. Veins extending to or nearly to the margin; apex of the terminal lobes entire or nearly so, with borders of elongate cells, scarcely protruding; spores deep brown ..... 13. *E. cheilanthoides.*
g. Veins terminating short of the margin; apex of the terminal lobes irregular, with the border cells irregularly protruding; spores light or deep brown. h.
h. Ultimate segments pubescent, the trichomes without glands (rarely glandular in intermediates); segment borders with irregular cells more or less projecting at the apex ..... 14. *E. hirsutulus.*
h. Ultimate segments hispid, with rigid, glandular trichomes; segment borders papillate with cells irregularly projecting at the apex ..... 15. *E. Lindigii.*
f. Lamina with rigid, bicolorous trichomes or glands; pinnae coriaceous. i.
i. Pinnae, at least in the lower portion of the lamina, elongate-ovate, often lobed; the margin plane, entire or deeply lobed .... 11. *E. setulosus.*

i. Pinnae orbicular, about as long as broad; the margins incurved or enrolled, crenulate ..... 12. *E. longipetiolatus.*

e. Leaves elongate-triangular, -ovate, or rhomboid, the central or lower pinnae about twice as long as the upper ones. j.

j. Leaves with tan or rust colored tomentum mostly obscuring the lamina surface or if sparsely pubescent, the pinnae stalks at least 1 cm. long; leaves scandent, scrambling, or if erect the pinnae sessile. k.

k. Basal pinnae with stalks 1–25 cm. long; rachis fractiflex; leaves with indefinite growth. l.

l. Vein ends terminating at the margin, often in a sinus ..... 17. *E. accrescens.*

l. Vein ends terminating in a tooth protruding from the segment margin ..... 16. *E. aureonitens.*

k. Basal pinnae sessile or with stalks less than 1 cm. long; rachis straight or nearly so; leaves with determinate growth ..... 18. *E. Stuebelii.*

j. Leaf surfaces clearly apparent, the lamina glabrous, pubescent or glandular; leaves usually erect. m.

m. Leaves distant on the rhizome, the internodes elongate. n.

n. Lamina texture herbaceous to chartaceous; the vein ends not or scarcely enlarged, rarely subclavate ..... 4. *E. paucifolius.*

n. Lamina texture rigid, coriaceous; vein ends enlarged to broadly clavate. o.

o. Pinnules with a broad, strongly decurrent base; pinnae elongate-triangular (the length exceeding twice the breadth); leaf buds (croziers) often large with dense, tan tomentum 9. *E. novogranatensis.*

o. Pinnules narrowed at the base, often stalk-like; pinnae deltoid, the length less than twice the breadth; leaf buds small, glabrous or nearly so ..... 8. *E. Warscewiczii.*

m. Rhizome with leaves closely placed, the internodes short, compact. p.

p. Veins terminating at or near the margin in a lobe or sinus. q.

q. Rachis and upper part of the petiole tan or straw colored. r.

r. Ultimate segments usually plane, with obtuse, mostly emarginate apices ..... 1. *E. myriophyllus.*

r. Ultimate segments incurved or enrolled, often bead-like with laciniate, usually acute apices ..... 2. *E. Sellowianus.*

q. Rachis and upper part of the petiole atropurpureous or castaneous. s.

s. Pinnae elongate-ovate or -triangular, with basal pinnules somewhat longer than the apical ones; the basiscopic side of the pinnae usually larger. t.

t. Rachis flexuose; pinnae descending or at right angles to the rachis ..... 21. *E. insignis.*

t. Rachis usually straight; pinnae more or less ascending or at right angles to the rachis. u.

u. Lamina 3- or 4-pinnate; the pinnules elongate-ovate or -triangular; ultimate segments usually with strong bifid lobes. v.

v. Rhizome trichomes light or golden brown, 2 or usually 1 cell at the base, often crispate; spores deep brown 3. *E. congestus.*

v. Rhizome bristles deep brown or black, thickened, with several (3–8) cells at the base, rigid, erect; spores tan or light brown ..... 5. *E. hirtus.*

u. Lamina 2-pinnate, the pinnules ovate or cuneate with few, shallow lobes, the margins crenate, retuse or more deeply cleft ..... 10. *E. rufescens.*

s. Pinnae lanceolate, the basal pinnules not or slightly longer than the apical ones; pinnae equilateral ..... 7. *E. velleus.*

p. Veins terminating in a lobe short of the margin. w.
w. Segment margins with a prominent, yellowish rim; upper surface of the lamina pubescent or glandular with rigid, erect trichomes ..... 6. *E. hispidulus.*
w. Segment margins not or scarcely differentiated; upper surface of the lamina glabrous or sparsely pubescent with lax, patent trichomes. x.
x. Ultimate segments orbicular with few, coarse lobes ..... 19. *E. Wurdackii.*
x. Ultimate segments cuneate, usuall with bifid lobes 24. *E. Biardii.*

1. **Eriosorus myriophyllus** (Sw.) Copel. Gen. Fil. 58. 1947

Fig. 10, Map 2

Gymnogramma myriophylla Sw. Vet. Akad. Handl. 58. 1817. TYPE: *Freyreis,* Brazil, Villa Rica (now Ouro Preto). August 1815. S-PA!, photo GH; isotypes: S-PA! photo GH; BM-frag!

Cheilanthes glandulosa Fée, Gen. Fil. 158. 1852. (non Swartz, 1817, *Paesia*). TYPE: *Claussen,* Brasilia, ex char. "indusio obsoleto, sporis trigonis."

Cheilanthes glandulifera Moore, Ind. Fil. 242. 1861 (non Liebm., 1849) based on *Cheilanthes glandulosa* Fée. Moore's name was taken up by Fée, Crypt. Vasc. Brés. 1:55. 1869, but not as a new name as accepted by some authors.

Anogramma villosa Fée, Crypt. Vasc. Brés. 1:60. 1869. TYPE: *Claussen,* in 1841, Brazil, Minas Geraes P! photo GH; nomen nud. Gen. Fil. 184. 1852.

Psilogramme myriophylla (Sw.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 339. 1882.

Gymnogramma myriophylla Sw. var. *eglandulosa* Rosenst. Hedwigia 46:148. 1906. TYPE: *Schmalz 132,* Brazil, Santa Catarina, Tresbarrassera, Herb. Rosenst. S-PA! isotype: NY! The specimen at S-PA is probably the holotype but does not bear the varietal name.

Gymnogramma myriophylla Sw. var. *eglandulosa* f. *flexuosa* Rosenst. Hedwigia 46:148. 1906. TYPE: *Jürgens & Stier,* Brazil, Rio Grande do Sul, Serra de Melo, Dec. 1903. S-PA; isotype: as *Jurgens 154,* NY!

Gymnogramma Glaziovii C. Chr. Ark. Bot. II 9(11):20. 1910. Based on *C. glandulosa* Fée (non Swartz, 1817).

Gymnogramma Felipponei Hert. Darwiniana 1:159, t. 160. 1924; An. Mus. Nac. Montevideo 1:356, t. 25, fig. a–g. 1925. TYPE: Anonymous n. 36 et 452 Jan. 1877, Uruguay, Sierra Souza, Cerro Largo, MUM.

Rhizome repent (often compact and quite erect at the apex), with short internodes, ca. 3–5 mm. in diameter, with trichomes or bristles crispate, ruddy brown, sometimes rigid, appressed, darker at the base, 1–4 cells wide, 1–2 cells thick, the apical cell globose, usually glandular. *Leaves* erect, 5–95 cm. long. *Petiole* plane or channeled on the upper surface, castaneous to straw colored, from 1/8 as long to equal the length of the lamina with sparse to dense pubescence, the trichomes short and erect or long and crispate, clear or tan, the apical cell globose, glandular. *Lamina* elongate-triangular or -trullate, the central pinnae usually longer than those at the base or apex. 3-pinnate, 2.5–67.0 cm. long, 0.5–16.0 cm. wide, determinate, the apical bud minute. *Rachis* straight, rarely somewhat fractiflex, the upper surface channeled, the lamina decurrent near the apex, sometimes slightly at basal

pinnae, castaneous to straw colored, densely pubescent, the trichomes clear or light brown, the apical cell globose, usually glandular. *Pinnae* at right angles to the rachis or somewhat ascending, elongate-triangular, rarely ovate, the basiscopic side slightly larger, 0.25–10.0 cm. long, 0.2–3.5 cm. wide, delicate herbaceous or somewhat membraneous; *upper surface* sparsely to densely pubescent, the trichomes clear, mostly short, glandular, the apical cell globose, sometimes subglobose, rarely eglandular; *lower surface* with similar trichomes usually sparser than on the upper surface; *stalk* 0.5–5.0 mm. sometimes with decurrent lamina tissue; *pinnules* elongate-ovate or -triangular; *ultimate segments* ovate with several large lobes, these often bifid, the apex retuse or more deeply cleft, plane; *veins* terminating in a cleft at the margin, not or slightly enlarged; *border* narrow, clear, 1 cell wide, the cells elongate, at the apex about as long as broad. *Sporangia* mostly on the penultimate vein and next order near the rachis, the stalk short, of one tier subtended by a tier or cushion of usually brown cells, the annulus of 12–21 indurated cells. *Spores* deep brown, the proximal face quite smooth, with ridges appressed to the triradiate scar, with a moderately broad equatorial flange, the angles often two-lobed, the distal face with a large, usually smooth, central areola, sometimes with the three ridges nearly parallel to and with the ends projecting into the equatorial flange.

Field studies in Brazil indicate that the species has a broad ecological tolerance as the plants occur in humid to xeric situations and at altitudes ranging from 600–2300 m. The compact form and growth of the rhizome are unusual because it is often deeply embedded in heavy, laterite soils. The plants apparently are adapted for survival under dry conditions and possibly light burning which is frequent in some areas where they grow. They are abundant on recently exposed soils along road banks and trails. At the highest point along the trail above the city of Ouro Preto, there were specimens of all sizes including some young ones with deteriorated gametophytes still adherent.

Meiotic chromosomes have been examined in material collected near Palmares, *Tryon & Tryon 6745* (GH), and although a precise number cannot be reported it is probably between 63–87 bivalents, and is tentatively given as 87. This population and others from Brazil should be checked because lower chromosome levels may be expected in the species. *Eriosorus myriophyllus* contrasts particularly with species of the Andean region and five others of Brazil in being exceptionally uniform morphologically. Only a few collections from Rio Grande do Sul and Paraná are distinctive in having a more delicate leaf texture and eglandular trichomes. They may represent different cytotypes but they are small specimens from rocky sites and are more likely to be depauperate forms.

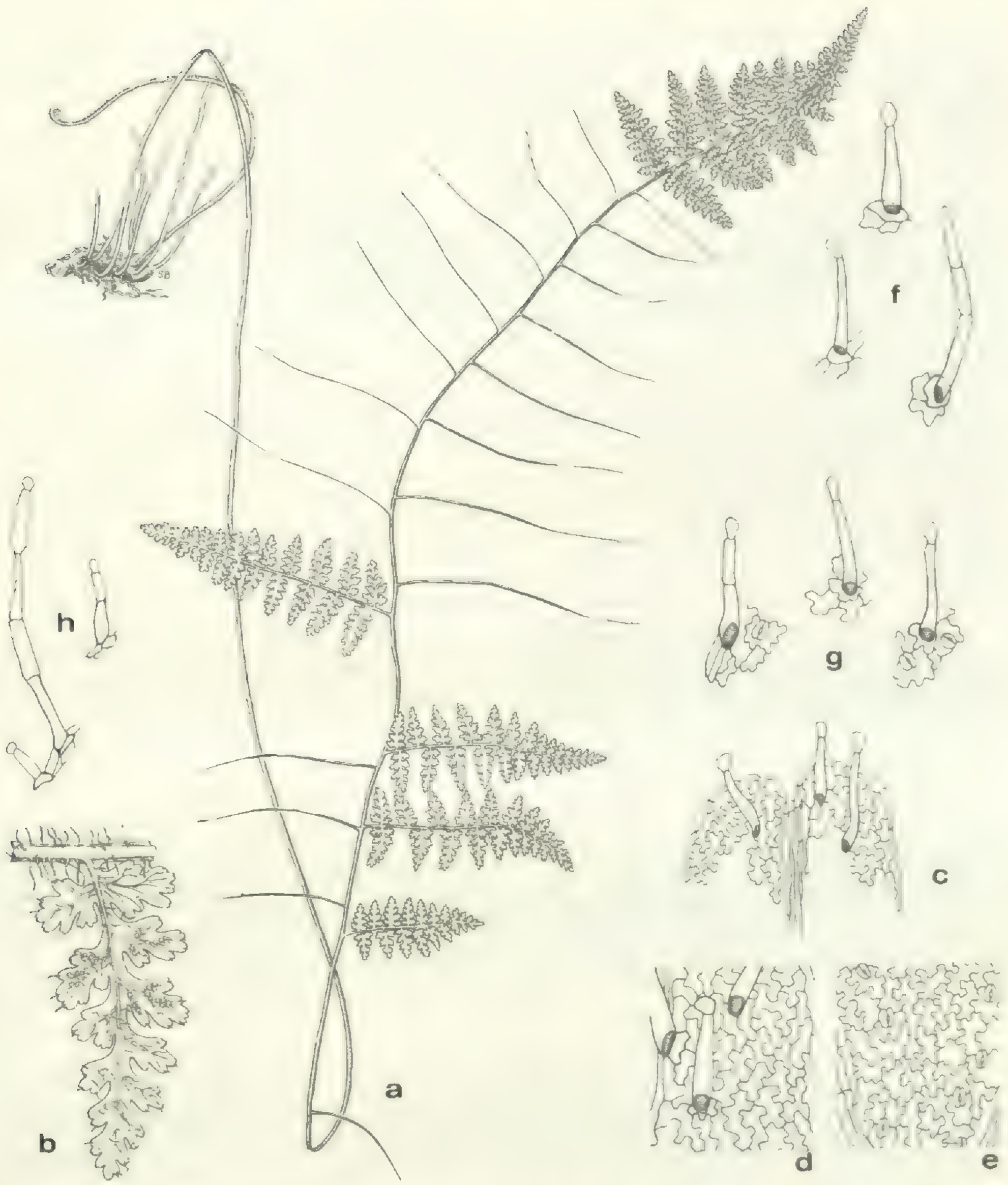


FIG. 10. *Eriosorus myriophyllus:* a, habit with few pinnae in detail and rachises of others, × 1/3; b, pinnule, × 2 both *Tryon & Tryon 6877* (GH); c, margin with vein end and glandular trichomes, × 34; d, upper epidermis with trichomes; e, lower epidermis with portion of veins; f, lamina trichomes, upper surface; g, lower surface, all × 40; h, rhizome trichomes, × 20, all from *Tryon & Tryon 6718* (GH).

This species is most closely related to *Eriosorus Sellowianus*, a more specialized type from the drier areas in Minas Gerais. In the erect orientation of the rhizome apex, it is similar to *E. congestus* and there are other similarities between them in the details of the pinnae. These two species have the most generalized leaf form which is regarded as the least modified and is the basic form in the genus. The spores of *E. myriophyllus* and *E. Sellowianus* also have sculpture aligned more like the banded spores of *Anemia*.

In shade beside streamlets, on damp shaded sandstone, in open or shrubby growth on roadbanks. Brazil and Uruguay, at 600–2300 m.

ADDITIONAL SPECIMENS EXAMINED: **Brazil. Minas Gerais:** *Badini 123* (RB), Itacolomy, *2824* (S, US); Serra do Caparaó, *Brade 17096* (NY), Serra do Cipó, *14397* (C, BHMG, RB); *Claussen 102* (G, P), *278* (B, BM); Ouro Preto, *Glaziou 15738* (B, C, K, P); Belo Horizonte, *Markgraf et al. 3554* (B, RB); Diamantina, *Mexia 5845a* (C, GH, US); Caldas, *Mosen 2241* (P, S, S-PA); Villa Rica, *Pohl 3649* (W); Serra de Capanema, *Schwacke 9258* (P), Ouro Preto, *14593* (P); *Silveira 52* (R); *Silveira & Thomar,* April 1896 (S-PA); Tripui, 4 km. W. of Ouro Preto, *Tryon & Tryon 6848* (GH), Serra do Ouro Preto, *6877* (GH), Itacolomy, *6881, 6882* (GH); *Weddell 1569* (P). **Rio de Janeiro:** Itatiaia, *Brade 6503* (NY, US), *10050* (R, RB), *10165* (BM, R, RB), *14495* (RB), *15537* (BM, NY, RB); *Campos Porto 2252* (RB); near Rio, *Burchell 2215* (GH, K, S-PA); Organ Mts., *Gardner 102* (BM, E, G, P, W); *Glaziou 5322* (B, C, K, NY frag., P, S, W), Itatiaia, 5323 (B, C, HBK, K, P, US), *7018* (B, K, P), *7019* (P); Serra Estrella, *Luetzelburg 12914* (S-PA); near Palmares, *Pabst 7330* (HB); Itatiaia, *L. B. Smith 1465* (GH, US), *1795* (C, GH, US); Serra do Estrella, *Spannagel,* in 1921 (NY); Itatiaia, *Tryon & Tryon 6718* (GH), near Palmares, *6745* (GH). **Sao Paulo:** Campos de Jordão, *Bailey & Bailey 808* (US); *Campos Porto 3109, 3110* (RB); *Leite 3484* (A), *3879* (A, GH); Serra de Cubatão, *Lindberg 22* (B); Campos da Bocaina, *Loefgren 21573* (NY); *Perdonnet 541* (G); Campos de Jordão, *Tryon & Tryon 6917* (GH); *Usteri,* 1906 (NY, SP); Pico de Itapeva, *Vital,* Mar. 1966 (GH); Rio Grande, *Wacket,* 1905 (GH, K, P, R), 1906 (B, E, P, S, S-PA, US). **Paraná:** Herb. Capanema, April 1877 (BM, RB); Villa Nova, *Annies 7* (NY); Serra S. Luiz, *Brade 19489* (RB); Fortaleza, *Dusen 2900* (P), Ypiranga, 3375 (BM, P, R, S), *7477* (S), Riv. Tibagy, *3488* (S), Villa Velha, *4028* (GH, P, R), *14908* (S), Iratý, *7811* (BM, S, S-PA, US), Serra do Mar, *14434* (B, BM, F, G, S); Serra de S. Luiz de Purunã, *Pabst 5915* (GH, HB); Carambehy, *Schwacke 1765* (P). **Santa Catarina:** Lages, *Spannagel 106* (S-PA); Bom Retiro, Campo dos Padres, *Smith & Reitz 10400* (US); Serra Geral, *Ule 2350* (P). **Rio Grande do Sul:** Gravatahy, *Dutra 160* (R), Bom Jesus, *259* (C, R); Rio Pardo, Faz. Agra, *Jurgens,* 1906 (B, BM, K, S, S-PA, US); Morro Sapucaina, *Leite 1702* (A); São Lepoldo, *Rick* (GH). **Uruguay.** Herb. *Arechavaleta,* 1875 (S-PA). **Cerro Largo:** *Arechavaleta 455, 2015* (P).

2. **Eriosorus Sellowianus** (Kuhn) Copel. Gen. Fil. 59. 1947

FIG. 11, MAP 3

Gymnogramma Sellowiana Mett. ex Kuhn, Linnaea 36:69. 1869. TYPE: *Sello 1365,* Brazilia, Herb. Mett. B! photo GH; isotype B! photo GH.

Psilogramme Sellowiana (Mett. ex Kuhn) Kuhn Fests. 50 Jub. Reals. Berl. (Chaetop.) 337. 1882.

Gymnogramma Schwackeana Christ, Pl. Nov. Mineiras 2:18. 1900. LECTOTYPE: *Schwacke 9398,* Brazil, Ouro Preto, P!; isolectotype: GH-frag.; Paratypes: *Schwacke 7564;* Serra do Ouro Preto, Herb. Christ P!, EM!; Serra de Ibitipoca, *Schwacke 12304* P! photo GH; Ouro Preto, *Schwacke 11302* P! photo GH.

Eriosorus Schwackianus (Christ) Copel. Gen. Fil. 59. 1947.

Rhizome repent, with short internodes, ca. 3–5 mm. in diameter, with trichomes or bristles crispate, sometimes rigid, light or golden brown, at the base 1 or 2 cells, the apical cell globose, glandular. *Leaves* erect, 5–76 cm. long. *Petiole* plane or channeled on the upper surface, castaneous to straw colored, from 1/8 to 1/3 as long as the lamina, with sparse to dense pubescence, the trichomes mostly short and erect or longer and crispate, clear, brown or bicolorous, the apical cell globose, glandular. *Lamina* linear-lanceolate, the central pinnae slightly broader, the basal ones usually withered, 2-pinnate, rarely 3-pinnate, 3–57 cm. long, 0.6-4.5 cm. wide, determinate, the apical bud minute. *Rachis* straight, the upper surface channeled, the lamina slightly decurrent at the pinnae axils, castaneous to straw colored, densely pubescent, the trichomes clear or light brown, the apical cell globose, glandular. *Pinnae* slightly to strongly ascending, elongate-triangular to -ovate, sometimes linear, equilateral, 0.3–3.0 cm. long, 0.3–1.6 cm. wide, membranaceous or coriaceous, rarely more delicate, subsessile; *upper surface* sparsely pubescent to nearly glabrous, the trichomes clear, the apical cell globose, glandular; *lower surface* sparsely pubescent, the trichomes similar to those on the upper surface; *stalk* 0.5–2.0 mm. sometimes with decurrent lamina tissue; *pinnules* orbicular or ovate, often enrolled and bead-like with few large, bifid lobes, the apex deeply cleft, laciniate; *veins* terminating in a cleft at the margin, slightly enlarged; *border* narrow, clear, 1–3 cells wide, the cells sometimes prolonged into glandular trichomes, those at segment apex irregular, often protruding from the margin. *Sporangia* along the veins often short of the ultimate division, most abundant on the penultimate veins and next order near the rachis, the stalk short, of 1 tier subtended by a tier of usually brown cells, the capsule of 12–19 indurated cells. *Spores* deep brown, the proximal face quite smooth with ridges appressed to the triradiate scar, with a moderately broad equatorial flange, the angles often projecting in two shallow lobes, the distal face with a large, usually smooth central areola, the three ridges nearly parallel to and with ends projecting into the equatorial flange.

Constant features characterizing these plants of Minas Gerais include pinnules with dense glands and laciniate margins. The coriaceous leaf texture and bead-like enrolled pinnules are usual but less constant aspects which seem to reflect the xeric habitats in which the plants usually occur. The relationship of this species to *E. myriophyllus* is relatively close. There seems to be no evidence of the kind of variation that is associated with hybridization. The specialized form of pinnules noted above shows a derived state as compared to *E. myriophyllus*. *Eriosorus Sellowianus* is the only clearly differentiated taxon that occurs within the geographic area of *E. myriophyllus*, which ranges from Minas Gerais in Brazil south to Uruguay. These two species provide a standard of differentiation for comparison of variation in the hybrid complexes among the Andean species.

Among rocks on planalto, in exposed places or sometimes overgrown by shrubs. Minas Gerais, Brazil, at 1450–1550 m.

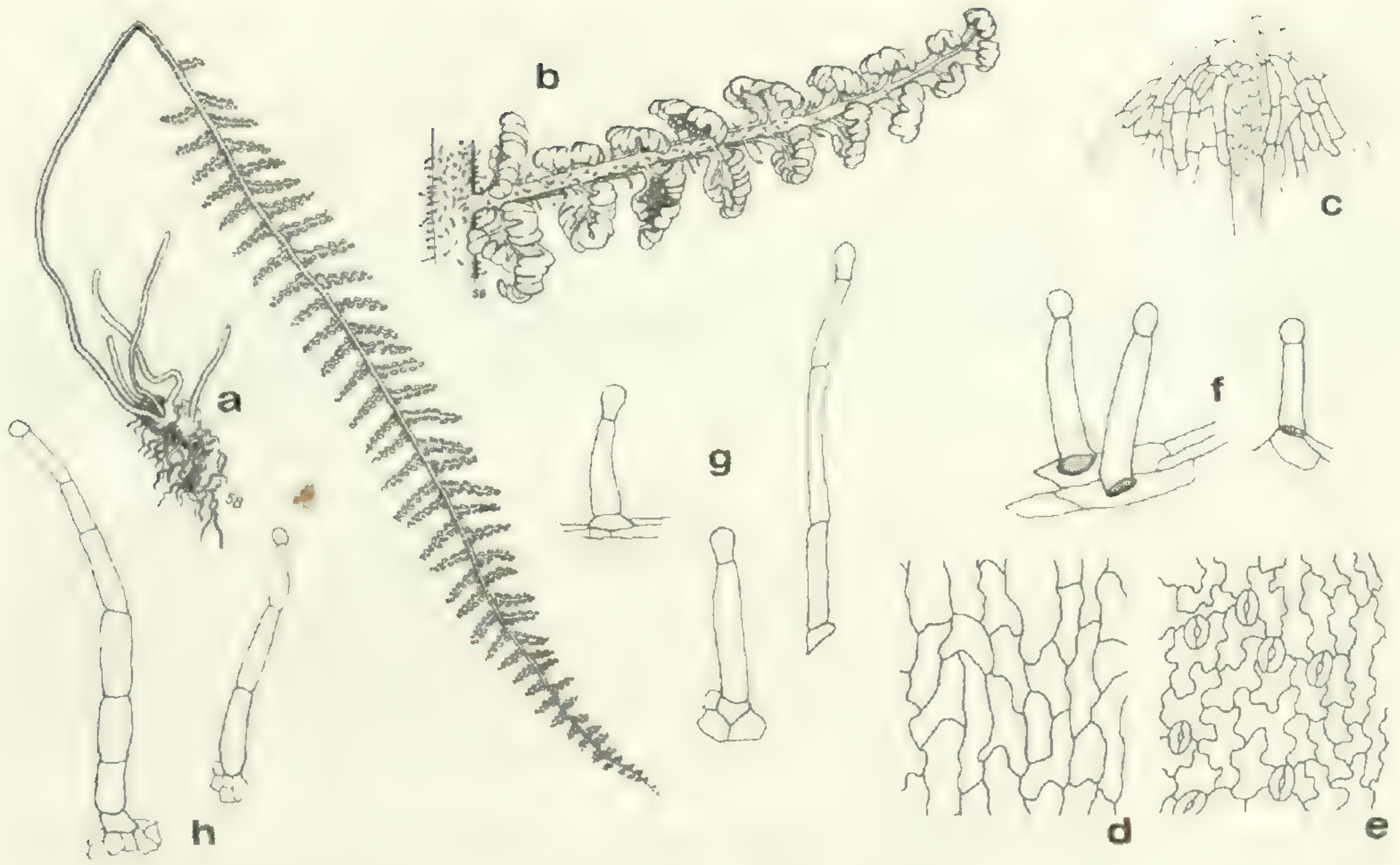


FIG. 11. *Eriosorus Sellowianus:* a, habit, × 1/3, *Glaziou 15737* (K); b, pinna, × 6, *Magalhães 1779* (GH); c, margin with vein end, × 20; d, upper epidermis; e, lower epidermis; f, g, lamina trichomes, f upper surface, g lower surface along vein, all × 40, from *Glaziou 7312* (P); h, rhizome trichomes with epidermal cells of rhizome at base, × 20, *Glaziou 15737* (K).

ADDITIONAL SPECIMENS EXAMINED: **Brazil. Minas Gerais:** Serro do Cipó, *Brade 14398* (BHMG, BM, F, G, NY, RB); Itacolomy, *Damazio* (NY-part) *1248* (P, R, RB), *1260* (R), *1784* (P), *1784A* (NY); Caraça, *Foster 710* (GH, US); Serra do Piedade, *Glaziou 7312* (K, P), *15737* (B, C, G, K, NY-frag.), *20584* (B, BM, C, K, P); near Rio Preto, *Mendes Magalhães 56* (R), Alto do Pico do Itambé, *1779* (BHMG, GH), *1810* (BHMG, HB); Cachoeira do Campo, *Schwacke,* April 1906, (BM), Serro do Campanema, *9258* (P), Serra do Piedade, *9777* (P, RB), Ouro Preto, *10701* (P, RB), *12745* (BM, NY, P, RB), *12745a* (P, RB), Serra do Cachoeira, *14417* (P, RB); Caraca, *Vainio 33257, 33262* (GH, TUR); Serra do Piedade, *Warming,* 1866 (BM).

3. **Eriosorus congestus** (Christ) Copel. Ind. Fil. 58. 1947

FIG. 12, MAP 4

Gymnogramma congesta Christ, Bull. Herb. Boiss. II, 4:1098. 1904. TYPE: (Chosen by Maxon) *Tonduz 12575,* Costa Rica, La Palma, 1459 m., Sept. 1898, P!; isotypes: G! US!; paratype: *Wercklé,* Costa Rica, P, photo GH.

Psilogramme congesta (Christ) Maxon, Bull. Torrey Club 42:81. 1915.

Rhizome repent (often compact and strongly erect at apex), with short internodes, ca. 2–7 mm. in diameter, with crispate, golden brown trichomes or bristles, at the base usually with one or sometimes two cells, the apical cell elongate. *Leaves* erect, 7–105 cm. long. *Petiole* plane or channeled on the upper surface, castaneous to atropurpureous, usually 1/3 to 1/4 longer than the lamina or sometimes equal to it, with sparse to dense pubescence, the

trichomes crispate, usually tan or clear, the apical cell usually elongate, sometimes globose. *Lamina* elongate-triangular or -ovate, the basal pinnae usually longest, 3-pinnate, 4–50 cm. long, 2–10 cm. wide, determinate, the apical bud minute. *Rachis* straight, the upper surface channeled, the lamina decurrent at least near the apex, castaneous, densely pubescent, the trichomes clear or tan, the apical cell usually elongate, sometimes globose. *Pinnae* slightly ascending, the basal ones often strongly ascending, elongate-triangular or -ovate, the basiscopic side usually larger, 0.5–9.0 cm. long, 0.3–4.0 cm. wide, rigid herbaceous; *upper surface* moderate to densely pubescent, the trichomes clear, the apical cell globose or elongate; *lower surface* with similar but longer trichomes, those between the veins usually with globose apex; *stalk* 0.5–5.0 mm. usually with decurrent lamina tissue; *pinnules* elongate-ovate or triangular; *ultimate segments* usually cuneate, with slender, scarcely spreading or bifid lobes about as long as broad, the margins retuse, plane or slightly enrolled; *veins* terminating in a sinus at the margin, slightly enlarged to clavate; *border* narrow, clear, one cell wide, the cells elongate, those at the apex about as broad as long to nearly two times longer than broad. *Sporangia* along the vein, usually more abundant on the penultimate veins and those of the next order near the rachis, the stalk with one or two tiers of clear cells, sometimes with a cushion of brown cells, the annulus of 17–25 indurated cells. *Spores* deep brown, the proximal face with prominent ridges or tubercles parallel to the triradiate scar, with a moderately broad equatorial flange, the angles not or slightly projecting, the distal face with few prominent tubercles within the central areola.

This is the most abundant of the Costa Rican species, growing largely at lower altitudes beyond the range of the others. It is common along road banks, on mossy turf, often in shaded sites but appears to be tolerant of open sun and drier, clay soils. In the Cordillera Central and the Talamanca Range it grows in cut-over woodlands in the cloud forest, and thrives in deforested areas, apparently invading the open places. Evidently the species reproduces freely from spores because there are abundant young plants in these areas. At La Palma it is frequent, especially at the bases of tree stumps. Scandent plants of *Eriosorus glaberrimus* also occur here on the few remaining trees. A specimen intermediate between *E. congestus* and the former [*Tryon & Tryon 7612* (GH)], more closely resembles *E. glaberrimus* in its scandent habit and is treated as a hybrid under that species.

Cytological samples of five populations of *Eriosorus congestus* from the provinces of Heredia, Alajuela and Cartago uniformly have 87 bivalents at meiosis. This is regarded as a hexaploid level originating from a triploid and achieving a balanced cytological condition by the doubling of the chromosomes. The lower polyploid levels have not appeared in the populations sampled in Costa Rica.

Maps 2–5. Map 2, *Eriosorus myriophyllus*. Map 3, *E. Sellowianus*, both Brazil. Map 4, *E. congestus*. Map 5, *E. paucifolius*, p, var. *paucifolius*, s, var. *Steyermarkii*, n, var. *neblinae*; hybrid with *E. flexuosus* var. *flexuosus*, star.

Eriosorus congestus represents the least specialized form among the Costa Rican species on the basis of the elongate-triangular, 3-pinnate leaves with undifferentiated margins and the simple rhizome trichomes. These characters, as well as the nearly sessile, and often decurrent pinnae and dark brown spores, suggest that it is most closely related to the Brazilian *E. myriophyllus*.

Among mosses in open, cut-over woodlands in the cloud forest, in thickets or on road banks in mossy vegetation or soil. Costa Rica, at 1300–2340 m.

Additional specimens examined: **Costa Rica.** 1901–1905, *Wercklé* (MICH, S-PA), 1903 (GH), 207 (P). **Heredia:** Vara Blanca, between Poás and Barba volcanos, *Maxon & Harvey 8380* (S-PA); *Scamman 7048* (GH); slope of Volcán Barba, *Scamman & Holdridge 7922* (GH), La Paz, *7926* (GH); Volcán Barba, *Godfrey 66168a* (FSU); Vara Blanca de Sarapiqui, *Skutch 3518* (GH, K, S-PA); vicinity of Vara Blanca, *Tryon & Tryon 6995, 6997*

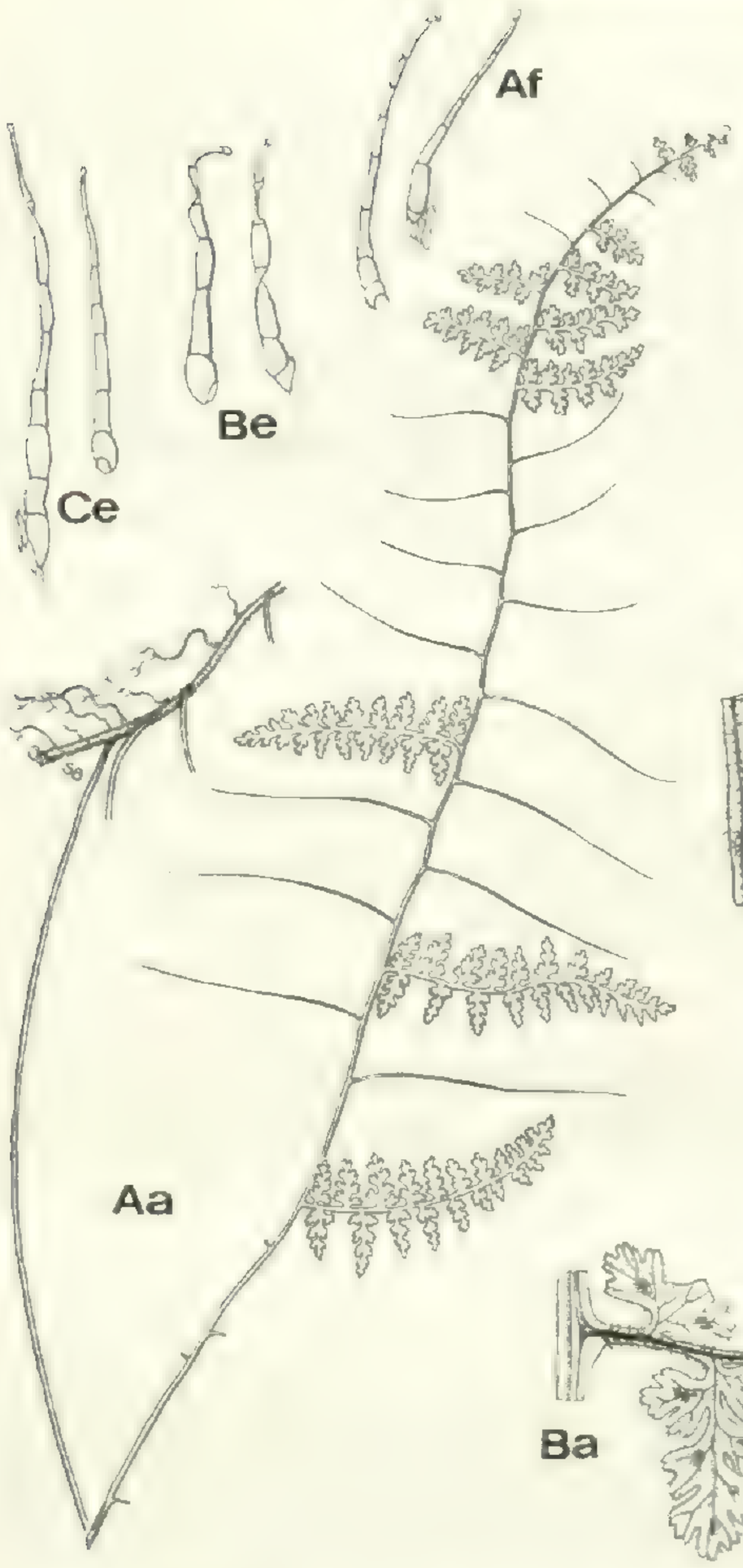
(GH), s.e. slopes of Barba, *7018* (GH). **Alajuela:** Poás, *Hunnewell 16508* (GH); *Alfonso Jiménez 821* (F); Palmira, *Austin Smith F79, H288, NY1410* (F); *Scamman 7625* (GH). **San José:** La Palma, *A. & Brade 85* (B, BM, P, S, S-PA, W); *Maxon & Harvey 7916* (GH, S-PA); road to San Cristobal, *Scamman 6074*, Las Nubes, *7047*, *Scamman & Holdridge 7921*, La Palma, *7623*, *Scamman 7624*, La Chonta, *Scamman & Holdridge 7923*, road to La Hondura, *7924* (GH); vicinity of El General, *Skutch 3048* (GH, K, S-PA); *Stork 2189* (MICH); San Cristobal road, La Hondura, *Werklé*, 1902, Herb. Inst. C.R. 16683 (GH, P), *17030* (P), *17048* (BM); 13 km. n. of San Isidro del General, *Tryon & Tryon 7047*, La Palma, *7063* (GH). **Cartago:** Santa Clara de Cartago, *Maxon & Harvey 8159* (S-PA); above El Empalme, *Molina et al. 17904* (F); *Tryon & Tryon 7044, 7056, 7059* (GH); near La Sierra, *L. O. Williams 16357 16464* (F), *Williams et al. 28108* (F, GH).

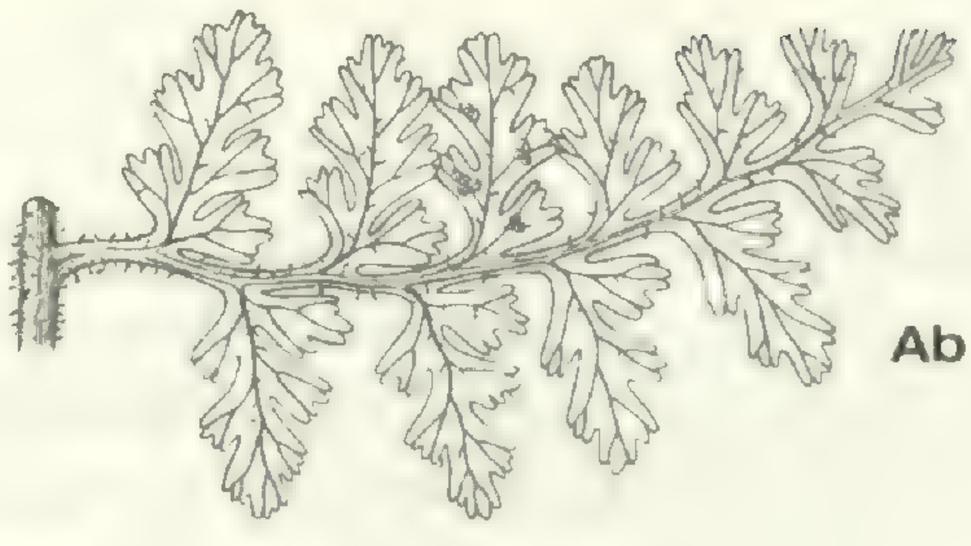
FIG. 12. *Eriosorus congestus:* a, habit with some pinnae in detail and rachises of others, × 1/3; b, pinna, × 1, both from *Tryon & Tryon 7018* (GH); c, margin with vein end and glandular trichomes, × 34, *Tryon & Tryon 7044* (GH); d, upper epidermis; e, lower epidermis; f, g, lamina trichomes, f lower surface, g upper surface, all × 40, from *Tryon & Tryon 6995* (GH); h, rhizome trichomes, ×20, *Tryon & Tryon 7003* (GH).

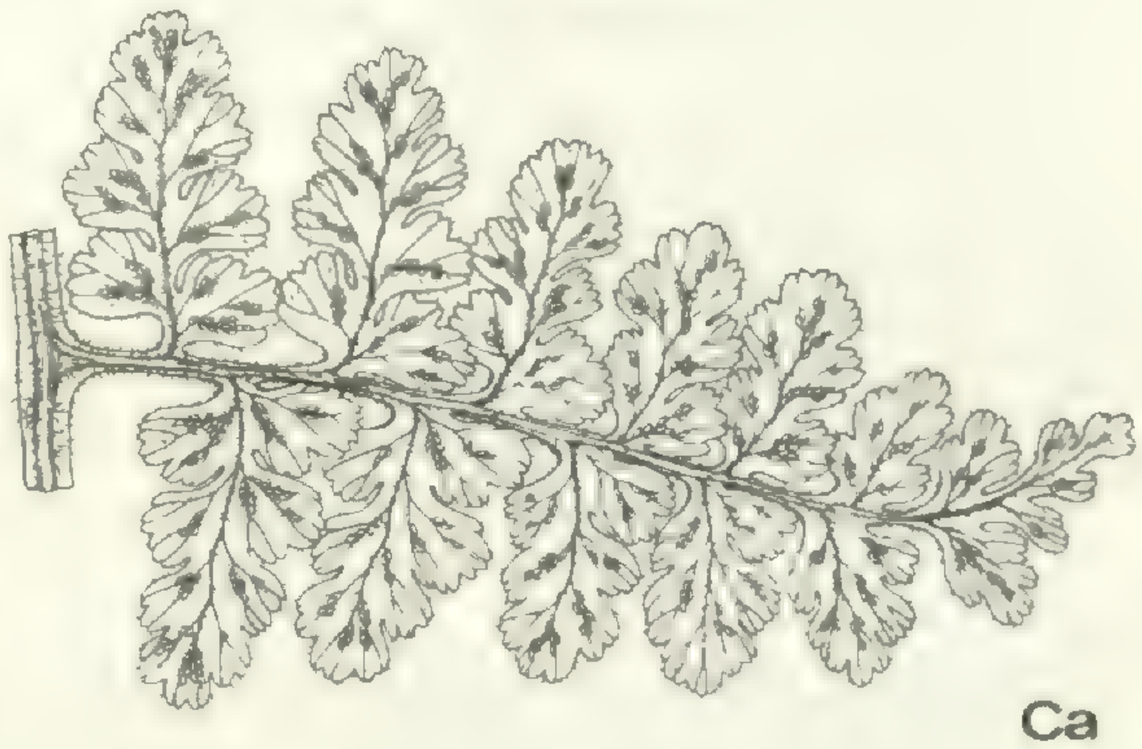
4. **Eriosorus paucifolius** (A. C. Smith) Vareschi, Fl. Venez. 1(2):641. 1969

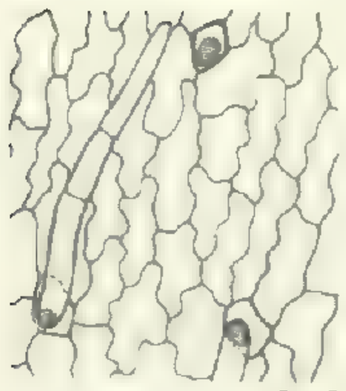
Rhizome repent elongate, with long internodes, ca. 1.5–3.0 mm. in diameter, the trichomes or bristles rigid, appressed, ruddy brown, at the base one or two cells, the apical cell globose. *Leaves* erect, ca. 14–92 cm. long. *Petiole* subterete or plane on the upper surface, atropurpureous or dark brown, equal to about 1/3 as long as the lamina, usually densely glandular with short, clear or tan glands, the apical cell globose, also with some longer, darker trichomes. *Lamina* elongate-trullate, -ovate or ovate-lanceolate, the longest pinnae in the lower half of the lamina, the basal ones usually withered, the apex acuminate, usually 3- or sometimes 4-pinnate, 10–66 cm. long, 3–13 cm. wide, determinate, the apical bud glandular or pubescent, minute. *Rachis* straight or rarely subflexuose, the upper surface channeled, atropurpureous or castaneous, pubescent, the trichomes short, clear or tan, the apical cell globose, glandular. *Pinnae* at right angles to the rachis or slightly ascending, elongate- or oblong-triangular, the basiscopic side slightly larger, 0.5–9.0 cm. long, 0.3–3.0 cm. wide, herbaceous or chartaceous; *upper surface* usually slightly pubescent, the trichomes mostly short, erect, clear or tan, with the apical cell globose, glandular, or few longer, eglandular trichomes; *lower surface* pubescent, the trichomes similar, usually longer than those above; *stalk* 1–5 mm. with ridges continuous with those of the rachis, without decurrent tissue (the pinna rachis distinctly alate); *pinnules* ovate, or elongate-ovate, the *ultimate segments* cuneate, ovate or orbicular, often with few large, bifid, spreading or compact lobes, the margins retuse or emarginate and plane; *veins* terminating at the margin, slightly enlarged; *border* narrow, clear, usually one cell wide, the cells elongate, shorter at the vein ends, sometimes with glandular trichomes from enlarged basal cells. *Sporangia* few, mostly on the penultimate veins and on the basal part of the ultimate veins, the stalk of one tier on a cluster of clear cells, the annulus of 13–19 indurated cells. *Spores* deep brown, the proximal face with broad ridges adjacent to the triradiate scar, the equatorial flange narrow or moderately broad, sometimes slightly irregular, the three angles not projecting, the distal face smooth within the central areola or with a few large tubercles.

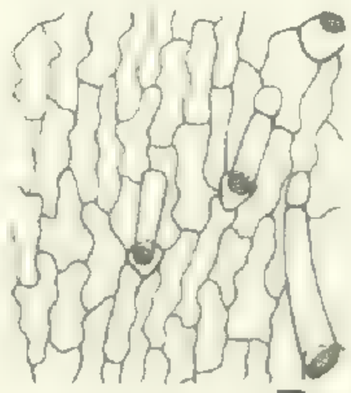
These collections from isolated Guayana massifs—Duida, Roraima, Ptari-tepuí and Neblina—are included under one species on the basis of similarities in several characters. They are alike in having slender rhizomes with long internodes and ruddy brown, uniseriate trichomes, the leaves with short, glandular trichomes on the lamina, and deep brown, sparsely sculptured spores. Differences in the division of the leaves and the shape of the ultimate segments in these are less relevant than the similarities noted above. Collections from the state of Bolivar, proposed as hybrids with this species under *Eriosorus flexuosus* var. *flexuosus* possibly involve var. *Steyermarkii*, which also occurs in Bolivar. The strongly fractiflex rachises in the Ule collection included under that variety also suggest a possible connection with *E. flexuosus*.

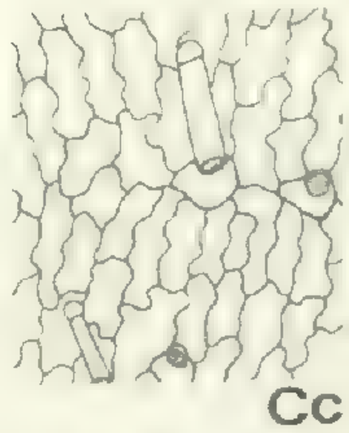


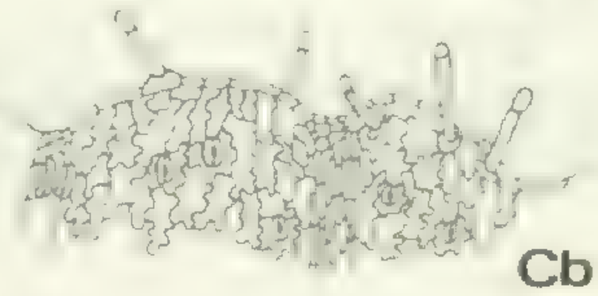


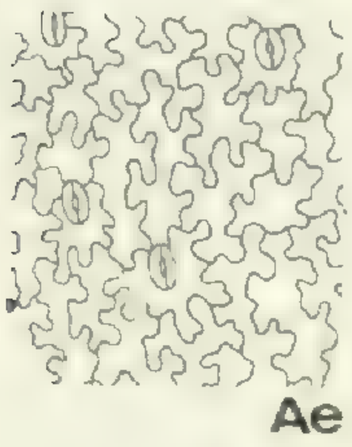


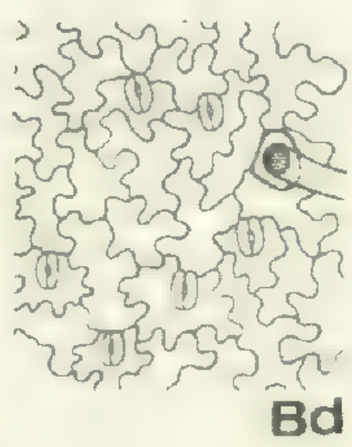


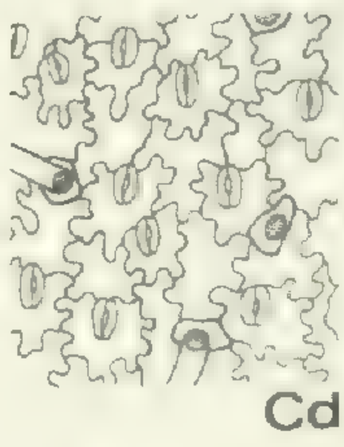












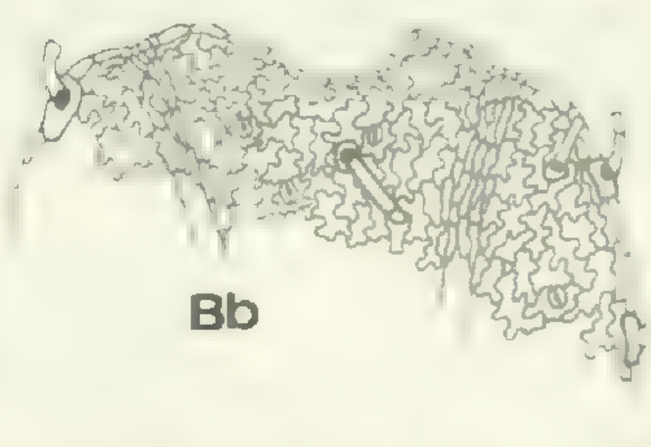


FIG. 13. *Eriosorus paucifolius.* Aa–Af var. *paucifolia:* Aa, habit with few pinnae in detail, rachises and basal stalks of the others, × 1/3; Ab, pinna, × 1–1/3; Ac, margin with vein ends, × 20; Ad–Ae, epidermis with trichomes, × 40; Ad, upper epidermis; Ae, lower epidermis; Af, rhizome trichomes, × 10, all from *Tate 677* (NY). Ba–Be var. *Steyermarkii:* Ba, pinna, × 4/5; Bb, margin with vein ends and glandular trichomes, × 20; Bc–Bd, epidermis with glandular trichomes, × 40; Bc, upper epidermis; Bd, lower epidermis, the basal cells of trichomes darker in both; Be, rhizome trichomes, × 10, all from *Steyermark 59913* (F). Ca–Ce var. *neblinae:* Ca, pinna, × 4/5; Cb, margin with vein ends and glandular trichomes, × 20; Cc–Cd, epidermis with glandular trichomes, × 40; Cc, upper epidermis; Cd, lower epidermis, basal cells of trichomes darker in both; Ce, rhizome trichomes, × 10, all from *Maguire et al. 37381* (US).

The relationship of these varieties to each other and to other species in the genus may be clarified as other collections become available. Some differences between them are shown in the epidermal cell patterns in Fig. 13, particularly in the smaller guard cell size in var. *neblinae*. A sample of ten guard cells from type collections shows an average 61.4μ in var. *paucifolius*, 60.2μ in var. *Steyermarkii* and 55.2μ in var. *neblinae*, which emphasizes the smaller size of the latter as is apparent in Fig. 13. The spores of var. *paucifolius* have a somewhat broader equatorial flange and are more irregular than the other varieties. This, along with sparse sporangia in these specimens, suggests some irregularity.

The slender rhizomes with elongate internodes and simple trichomes are similar to those of *E. Warscewiczii* and *E. novogranatensis*, but in other respects a close relationship is not indicated. The elongate, somewhat triangular leaves, simple rhizome trichomes and deep brown spores in *E. paucifolius* are unspecialized characters representing a relatively generalized and less advanced level in the genus.

KEY TO THE VARIETIES OF ERIOSORUS PAUCIFOLIUS

a. Pinnules slender, oblong-triangular and slightly broader at the base; the ultimate segments spreading, not imbricate, with deep, wide sinuses and somewhat prolonged lobes; the border of elongate cells, without trichomes ..... 4a. *E. paucifolius* var. *paucifolius*.

a. Pinnules broad, ovate; the ultimate segments compact, often imbricate, the sinuses shallow, the lobes rounded and blunt; trichomes along the border with large basal cells. b.

b. Lamina 4-pinnate, the ultimate segments cuneate with strongly spreading lobes ..... 4b. *E. paucifolius* var. *Steyermarkii*.

b. Lamina 3-pinnate, the ultimate segments mostly ovate or orbicular with compact lobes ..... 4c. *E. paucifolius* var. *neblinae*.

4a. Eriosorus paucifolius var. paucifolius

FIG. 13A, MAP 5

Psilogramme paucifolia A. C. Smith, Bull. Torrey Club. **58**:305. 1931. TYPE: *Tate 677*, Venezuela, Mt. Duida, Peak 7, 7050 ft. NY! isotypes: K!, US!

Gymnogramma paucifolia (A. C. Smith) C. Chr. Ind. Suppl. III. 109. 1934.

Lamina mostly 3-pinnate; *pinnules* oblong-triangular; *ultimate segments* widely spaced, cuneate, bilobate, emarginate, the lobes somewhat acute; *border* of elongate cells, without trichomes. *Spores* mostly well developed, the equatorial flange broad, often irregular.

Eriosorus paucifolius is still known only from the original collection upon

which the species was described. It is distinct from the others in having slender pinnules widely spaced on the rachis. The leaf texture is unusually delicately herbaceous for the species and the sporangia are very sparsely scattered on the veins. The field data, with the collection, note the plants as "terrestrial, on forest covered slope." This and the delicate texture suggest that the specimen may be a shade grown form. The spores have a somewhat broader, more irregular equatorial flange than those of other collections of the species.

4b. **Eriosorus paucifolius** var. **Steyermarkii** A. F. Tryon, var. nov.

FIG. 13B, MAP 5

Rhizoma internodiis longis trichomatibus ad basim cellula 1 latis, lamina trullata vel ovata ovato-lanceolata 3-pinnata apice determinato gemma leviter glandulifera, pinnae elongato- vel oblongo-triangulares segmentis ultimis distantibus cuneatis profunde retusis lobis rotundatis, margo segmentorum cellulis elongatis aliquot trichomatibus glanduliferis basaliter dilatatis, sporae atrofuscae.

TYPE: Venezuela, Bolívar, Ptari-tepuí, along base of south-facing high sandstone bluffs, 2410 m. Nov. 6, 1944, *Julian A. Steyermark* 59913, US; isotypes: NY, S, VEN.

Lamina 4-pinnate; *pinnules* ovate or elongate-ovate; *ultimate segments* mostly compact, closely spaced, or imbricate, cuneate, bilobate, often with deep sinuses and strongly spreading lobes; *border* of elongated cells and glandular trichomes with the basal cells larger than the adjacent border cells. *Spores* with a narrow, entire equatorial flange.

The trichomes along the segment borders differ relatively little from those of the lamina surfaces but have larger, more conspicuous basal cells. Modification of the segment borders is exceptional in this genus as compared to *Jamesonia* where the pinna margins are much elaborated. Specimens of the Ule collection have few glands along the border and the rachises are quite flexuose; thus, it is included with some reservation. The putative hybrid involving this species, included under *E. flexuosus* var. *flexuosus*, probably involves this variety since it occurs in Bolivar and on Mt. Roraima.

I am pleased to name this variety for Dr. Julian Steyermark, whose numerous collections of these ferns from the sandstone massifs and the Venezuelan highlands, as well as in Guatemala and Ecuador, has supplied many specimens vital to this treatment and to our knowledge of the American flora.

Among rocks, at base of and on main south-facing, high sandstone bluffs. State of Bolívar, Venezuela, at 2200–2400 m.

ADDITIONAL SPECIMENS EXAMINED: **Venezuela. Bolívar:** Ptari-tepuí, Oct. 30, 1944, *Steyermark* 59607 (F, NY, US, VEN); Roraima, Jan. 10, 1910. *Ule* 8513 (B, G, K).

4c. **Eriosorus paucifolius** var. **neblinae** A. F. Tryon, var. nov.

FIG. 13C, MAP 5

Rhizoma internodiis longis trichomatibus ad basim cellula 1 latis, lamina oblongo-rhombica 2-pinnata apice determinata gemma leviter glandulifera, pinnae oblongo-triangulares segmentis ultimis approximatis valde cuneatis

retusis lobis rotundatis, margo segmentorum cellulis elongatis trichomatibus paucis glanduliferis basaliter dilatatis, sporae atrofuscae.

TYPE: Venezuela, Amazonas, Rio Yatua, Cerro de la Neblina, on escarpment, slopes e. of Camp 3, 1600 m. Jan. 24, 1954, *Maguire, Wurdack & Bunting 37381*, US.

Lamina 3-pinnate; *pinnules* elongate-ovate; *ultimate segments* closely placed with a strongly cuneate base, the lobes compact and sinuses shallow; *border* with elongated cells and some glandular trichomes with enlarged basal cells. *Spores* with a narrow, entire equatorial flange.

This is the most distinctive member of the species in that it has a compact form of pinnule with shallowly lobed ultimate segments. It seems best placed with other rare collections in this species from isolated massifs in southern Venezuela. The well formed spores and smaller epidermal cells indicate that it may represent a lower ploidy level than the others. The limited record of this taxon contrasts with *E. flexuosus*, also found on Cerro Neblina, one of the most widely distributed and morphologically specialized species of the genus. In comparison to that species, var. *neblinae* is a less specialized, relict form, adapted to the forest slopes and escarpments of the Cerro.

5. **Eriosorus hirtus** (HBK.) Copel. Gen. Fil. 58. 1947

Rhizomes repent, compact with short internodes, ca. 4–9 cm. in diameter with the bristles or trichomes rigid, appressed, deep brown to black at the base, 1–8 cells wide, 1–5 cells thick, the apical cell elongate or globose. *Leaves* erect, 10–67 cm. long. *Petiole* subterete, usually channeled near the apex, atropurpureous to castaneous, usually longer (up to 2 times) or to 1/3 as long as the lamina, with sparse to dense pubescence, the trichomes crispate, clear, brown or bicolorous, the apical cell elongate or globose, glandular. *Lamina* elongate-triangular or deltoid, the basal pinnae longest, usually 3- or 4-pinnate, 4.5–45.0 cm. long, 2.5–22.0 cm. wide, determinate, the apical bud minute. *Rachis* straight, rarely subflexuose, the upper surface plane or channeled, the lamina decurrent at least near the pinnae, castaneous, sparsely to densely pubescent, the trichomes clear or light brown, the apical cell elongate or globose. *Pinnae* slightly ascending, elongate-triangular, or deltoid, the basiscopic side usually larger, 1.5–20.0 cm. long, 1–11 cm. wide, herbaceous; *upper surface* moderately to densely pubescent, the trichomes clear or tan, the apical cell elongate or globose, often with trichomes of both forms; *lower surface* moderately to densely pubescent, the trichomes similar to those on the upper surface; stalk 2–10 mm. long, sometimes with decurrent lamina tissue; *pinnules* elongate-ovate or triangular; *ultimate segments* cuneate, often with bifid lobes, the margins retuse or more strongly cleft, plane; *veins* terminating at or rarely short of the margin, scarcely enlarged or subclavate; *border* narrow, clear or opaque, 1–5 cells wide, sometimes with a slightly differentiated rim, the cells elongate, the marginal ones projecting at the apical end, those at the vein ends about as long as broad. *Sporangia* mostly on the ultimate, penultimate veins and next order near the rachis, the stalk short, one or two tiers of clear cells, the annulus of 12–19 indurated cells. *Spores* tan or light brown, the proximal face with papillae or short ridges adjacent to the triradiate scars, with a broad equatorial flange, the angles projecting, the distal face somewhat papillate or nearly smooth within the central areola.

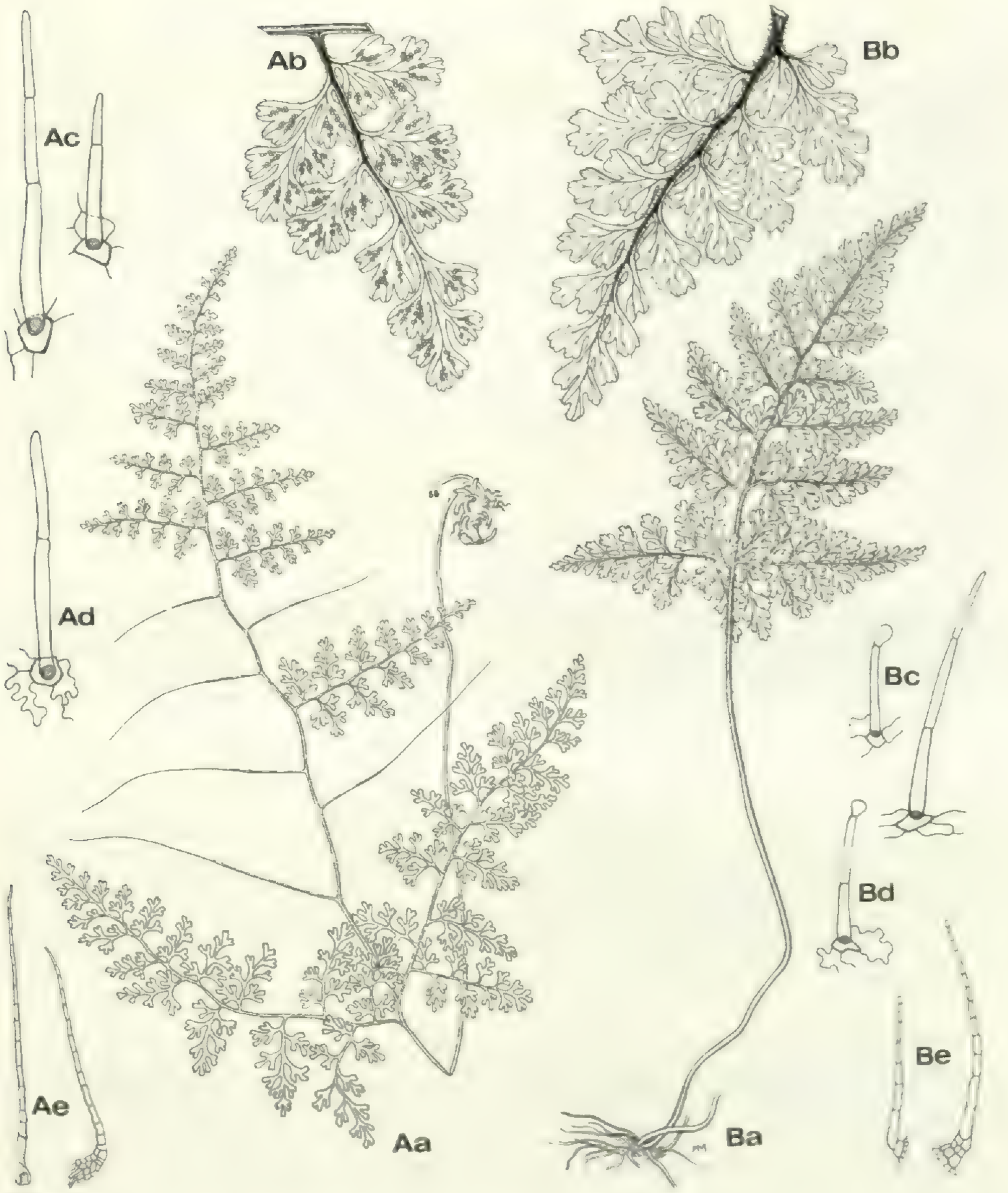


FIG. 14. *Eriosorus hirtus*. Aa–Ae var. *hirtus:* Aa, habit, × 1/3, *Steyermark 89839* (GH); Ab, pinna, × 2/3, *Williams & Alston 294* (GH); Ac–Ad, lamina trichomes, × 40, Ac upper surface, Ad lower surface, both *Steyermark 89838;* Ae, rhizome trichomes, × 10, *Pittier 9261* (GH). Ba–Be var. *glandulosus:* Ba, habit, × 1/3; Bb, pinna, × 2/3; Bc–Bd, lamina trichomes, × 40, Bc upper surface, Bd lower surface; Be, rhizome trichomes, × 10, all from *Alston 8238*(GH).

The geographic range of *Eriosorus hirtus,* although broad, is unusually disjunct, lacking records from all of Peru and Costa Rica. Robust specimens from the northern part of the range and from Bolivia and Cuba are included under var. *hirtus*. The smaller, glandular specimens from higher altitudes in Colombia and Ecuador, which appear to represent more specialized forms are

treated under var. *glandulosus*. Several variable collections from southern Colombia and southern Ecuador are treated as putative hybrids with *E. flexuosus*. The relationship of *E. hirtus* to *E. flexuosus* is significant because the highly complicated leaves in the latter could be elaborated from the simpler form of *E. hirtus* var. *hirtus*. The broad rhizome bristles, light spore color, and the undifferentiated segment borders are similar to *E. hispidulus*. In addition, the leaves of these two are generally similar but they are somewhat more compact in *E. hispidulus*. *Eriosorus hirtus* represents a relatively unspecialized morphological level in the genus.

KEY TO THE VARIETIES OF ERIOSORUS HIRTUS

Lamina elongate-triangular, usually more than twice as long as broad; lamina and rachis moderately to densely pubescent, the trichomes usually bearing an elongate, apical cell ..... 5a. *E. hirtus* var. *hirtus*.
Lamina deltoid, about as long as broad; lamina and rachis densely pubescent, the trichomes with a globose, capitate apical cell ..... 5b. *E. hirtus* var. *glandulosus*.

5a. Eriosorus var. hirtus

FIG. 14A, 15A, MAP 6

Grammitis hirta HBK. Nov. Gen. et Sp. 1:4. (Fol. ed.) 1816. TYPE: *Humboldt & Bonpland*, Venezuela, Silla de Caracas, P! in Herb. Gen. ex Bonpland, photo GH; isotype: *Humboldt & Bonpland*, fragment B!

Gymnogramma hirta (HBK.) Kaulf. Enum. 72. 1824.

Gymnogramma petroselinifolia Kze. ex Kl. Linnaea **20**:409. 1847. TYPE: *Moritz 95b*, Venezuela, Colonia Tovar, B! photo GH; isotype: BM! photos GH, S-PA, US.

Anogramma petroselinifolia (Kl.) Fée, Gen. Fil. **5**:184. 1852.

Psilogramme hirta (HBK.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 338. 1882.

Psilogramme chiapensis Maxon, Bull. Torrey Club **42**:81, 1915. TYPE: *Purpus 6722*, Mexico, Chiapas, Cerro del Boqueron, Sept. 1913, US!; isotypes: BM! F! GH! HBG! P! US!

Gymnogramma chiapensis (Maxon) C. Chr. Ind. Fil. Suppl. Prélim. 19. 1917.

Psilogramme cubensis Maxon, Jour. Wash. Acad. **12**:441. 1922. TYPE: *Leon 11111*, Cuba, Oriente, Sierra Maestra, Pico Turquino, July 1922, US!; isotype: NY!

Gymnogramma cubensis (Maxon) C. Chr. Ind. Fil. Suppl. III. 108. 1934.

Lamina elongate-triangular, 4- rarely 5-pinnate, 4.5–45.0 cm. long, 2.5–22.0 cm. wide, with moderate to sparse pubescence on both surfaces, the trichomes mostly with an acuminate apex or with some bulbous, glandular trichomes.

The geographic disjunction of this variety is peculiar as compared to ranges of other fairly widespread taxa within the genus. The absence of

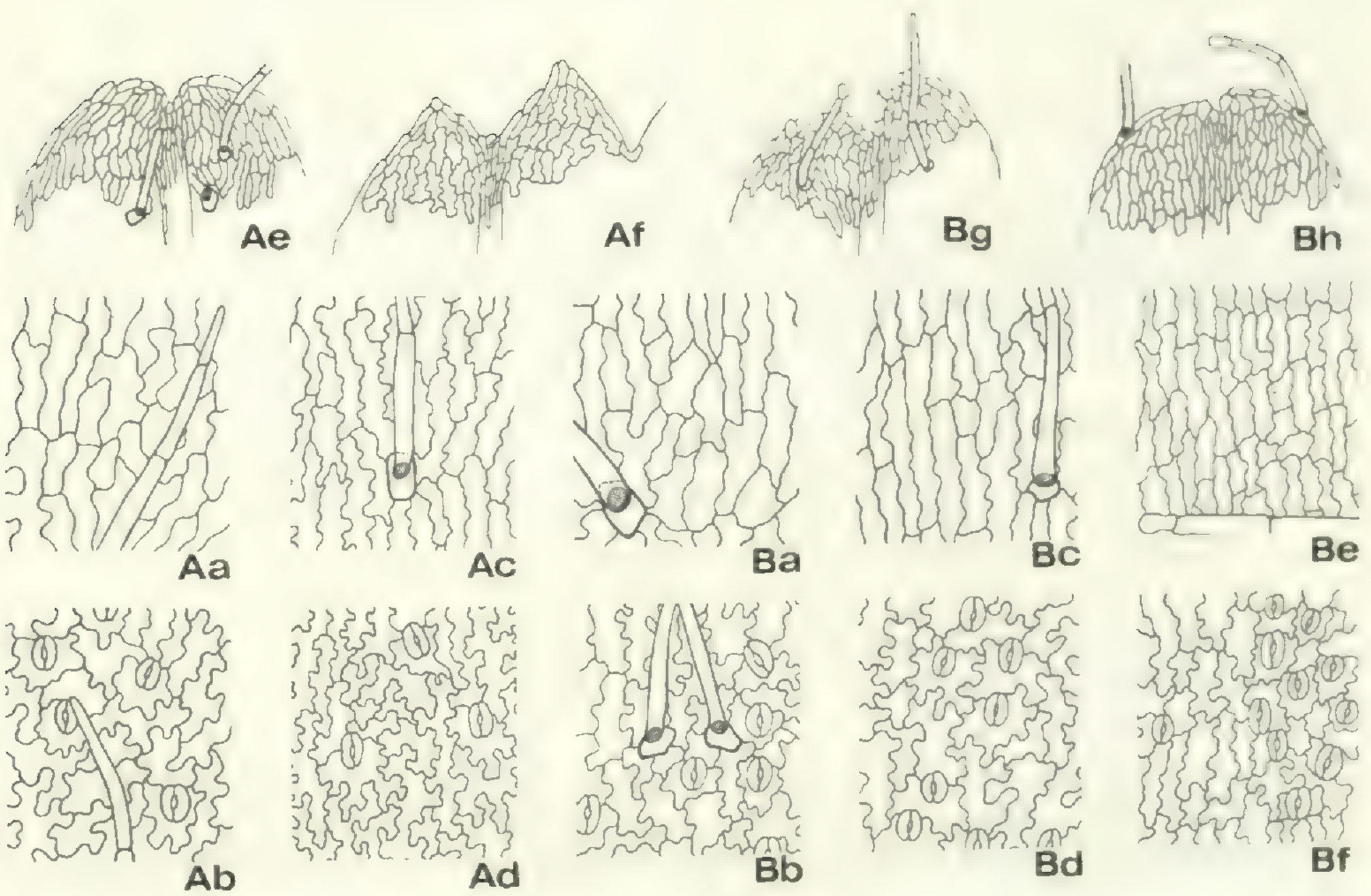


FIG. 15. *Eriosorus hirtus* and hybrids: epidermal cell walls and margins. Aa–Af var. *hirtus:* Aa–Ad, epidermis, × 40; Aa, Ac, upper epidermis; Ab, Ad, lower epidermis; Aa, Ab, with apical portions of trichomes, *Steyermark 89839* (GH); Ac, with basal portion of trichome; Ad, *Steinbach 9855* (GH); Ae, Af, margins with vein ends, × 20; Ae, with basal cells of trichomes, *Steyermark 89839* (GH); Af, *Steinbach 9855* (GH). Ba–Bd and Bg–Bh var. *glandulosus:* Ba–Bd, epidermis with trichomes, × 40; Ba, Bc, upper epidermis; Bb, Bd, lower epidermis; Ba, Bb, *Alston 8238* (GH); Bc, Bd, *Pennell & Killip 7319* (GH); Be upper epidermis, Bf lower epidermis of *E. hirtus* × *E. flexuosus, Pennell & Killip 7426* (GH); Bg, Bh, margins with vein ends and trichomes of var. *glandulosus,* × 20; g, *Alston 8238* (GH); h, *Pennell & Killip 7319* (GH).

specimens from Costa Rica may represent a real gap because the subalpine habitats in which these plants occur are relatively well sampled. Most collections from Venezuela lack glands on the leaves, but some having glands occur near Caracas. These specimens also show a considerable variation in leaf shape and in the form of the ultimate segments. Some specimens with fractiflex rachises and slender, bifurcate ultimate segments may represent intermediates involving hybridization with *E. flexuosus.*

Terrestrial, in upper subalpine forest, among shrubs or on roadside, 1700–2700 m. Southern Mexico, Central America, Cuba, Venezuela and Bolivia.

ADDITIONAL SPECIMENS EXAMINED: **Mexico. Chiapas:** Cerro del Boqueron, *Purpus 7219* (US); El Triunfo, Sierra de Soconusco, *Xolocotzi & Sharp X–470* (US). **Guatemala. Huehuetenango:** Sierra de los Cuchumatanes, *Steyermark 51954* (F, GH, US). **Honduras. Morazán:** above Rosario Mine, *Morton 7379* (US). **Venezuela. Sucre:** Cerro Turumuqire, *Steyermark 62651* (F). **Anzoátegui:** Cerro Peonia, *Steyermark 61596* (F). **Distrito Federal:** Los Venados, *Allart 108* (US); near Caracas, *Elias 11* (F); *Funck & Schlim 300* (G, in part K, P); Quebrada de Sollas, *Gollmer,* 1856 (B); Caracas, *Linden 73* (G, K, P); Silla de Caracas, *Pittier 8325* (GH, US, VEN); *Kuntze 74* (K, NY); *L. Williams 12361* (F, VEN); between Las Flores y Boca del Tigre, *Williams & Alston 294* (BM, GH, VEN). **Miranda:** Galipán, *Gollmer,*

1854 (B); *Pittier 6217* (US), *6498* (US); *Wagener 358* (B). **Aragua:** Colonia Tovar, *Allart 343* (NY, US, VEN); *Fendler 301* (B, BM, F, G, GH, K, NY), 358 (GH); *Gollmer 123* (B); *Moritz 95* (B, BM, E, G, GH, HBG, K, P, S-PA, W); *Pittier 9261* (GH, NY, US, VEN); around Tovar, *Vogl* (GH, S, US, W); parque Henry Pittier, above El Limón, *Steyermark 89839* (GH); *Tschudy 124* (VEN). **Bolivia. Cochabamba:** Prov. Chapare, *Steinbach 9855* (E, F, G, GH, NY, S-PA, US). **Cuba. Oriente:** Pico Turquino, *Ekman 5518* (G, NY, S, US), *14544* (S, US); *Seifriz 1130* (US).

5b. **Eriosorus hirtus** var. **glandulosus** (Karst.) A. F. Tryon, comb. nov.

FIG. 14B, 15B, MAP 6

Gymnogramma glandulosa Karst. Fl. Columb. 1:196, t. 97. 1861. TYPE: *Karsten,* Colombia, Cord. Bogotá, 2300 m. LE! photo GH; isotypes: B! photo GH, W! photo GH.

Psilogramme glandulosa (Karst.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 338. 1882.

Gymnogramma caracasana Bak., Syn. Fil. ed. 2, 516. 1874. Baker attributes this to Klotzsch (apparently unpublished) and also cites *G. glandulosa* Karsten, as a synonym; thus the name is superfluous.

Psilogramme caracasana (Bak.) Pitt. in Pittier, Lasser, et al. Cat. Fl. Venez. 1:36. 1945.

Eriosorus caracasanus (Bak.) Vareschi, Fl. Venez. 1(2):637. 1969. Illegit.

Lamina triangular or usually deltoid, 3-pinnate, 5-17 cm. long, 3–10 cm. wide, with dense indument on both surfaces, the trichomes mostly with bulbous, glandular apical cells, usually also some acicular with an elongate apex.

In addition to the characters distinguishing the two varieties of *E. hirtus* given in the key, there are differences in the lamina structure as shown in Fig. 14 which make an open, lax habit in var. *hirtus,* in comparison with the denser, more compact var. *glandulosus.*

On dry bank in upper rain forest, in brushy slopes and road banks, at 2200–2800 m. Colombia, Ecuador and Bolivia.

ADDITIONAL SPECIMENS EXAMINED: **Colombia.** Chimbe, 2200 m., *Lindig 136* (B, GH, K, P, US). **Cundinamarca:** Gachetá, *Grant 9470* (US); Bogotá, Páramo Cuervo, *Triana,* 1866 (G). **Cauca:** above Carpinteria, *Alston 8238* (BM, GH); San Antonio, *Pennell & Killip 7319* (GH, NY, S, US); Cerro Munchique, *Tryon & Tryon 5995* (GH). **Narino:** Volcán Cumbal, *Ewan 16150* (GH, NO, S, US). **Ecuador. Loja:** S. of Loja, *Wiggins 10877* (NY), w. of Loja, *10985* (NY, US). **Bolivia. Cochabamba:** above Tablas, *Herzog 2155* (B, S, US).

PUTATIVE HYBRID INVOLVING ERIOSORUS HIRTUS VAR. GLANDULOSUS

Eriosorus hirtus var. **glandulosus** × **Eriosorus flexuosus** var. **flexuosus**

The material believed to have arisen from the above hybrid combination has an indument similar to that of var. *glandulosus* and the elongate leaf form of *E. flexuosus.* The spores are irregular. Epidermal cell wall patterns and details of the leaf margins from the hybrid, cited below, are illustrated in Fig. 15B e, f, h. In these, the cells of the upper epidermis are unusually

Maps 6–9. Map 6, *Eriosorus hirtus*, var. *hirtus*, dot; var. *glandulosus*, rhomb; hybrid, *E. hirtus* var. *glandulosus* × *E. flexuosus* var. *flexuosus*, star. Map 7, *E. hispidulus* var. *hispidulus*, dot; var. *dominicensis*, rhomb.; hybrid, *E. hispidulus* var. *hispidulus* × *Jamesonia*, star; variants 1 & 2 as cited in text. Map 8, *E. velleus*. Map 9, *E. novogranatensis*, variant, rhomb.

small and the guard cells in the lower epidermis are variable in size and irregularly distributed. Data given with the specimens indicate that the hybrid is from a habitat intermediate to that of the probable parents. The following three collections were made at the same locality, within an altitudinal range of 2400–2700 m., on the same day. The collection of *E. flexuosus (Pennell & Killip 7367)* is scandent and is reported as growing in the forest. Their collection of *E. hirtus* var. *glandulosus (Pennell & Killip 7319)* with small, erect leaves, is from a dry, bushy hillside. The hybrid, cited below, has long erect leaves and is from a bushy forest. **Colombia. Cauca:** San Antonio, "San Jose," *Pennell & Killip 7426* (GH, NY).

The collection cited below resembles *E. hispidulus* and may key out to that on the basis of the veins ending short of the margin. However, there is some resemblance to *E. hirtus* in the 4-pinnate leaves with strongly bifid ultimate segments, and in the slightly fractiflex rachises to *E. flexuosus;* thus the specimen seems best placed here. **Ecuador. Loja:** Chinche, between San Pedro and Zaruma, *Penland & Summers 1183* (F).

A collection *(Killip & Smith 18195)* from the department of Santander, Colombia, treated as Variant 5 under *E. flexuosus* var. *flexuosus,* may also represent this hybrid, but there is no record of associated species.

6. **Eriosorus hispidulus** (Kunze) Vareschi, Fl. Venez. 1(2):640. 1969

Rhizome decumbent, compact with short internodes, ca. 2–8 mm. in diameter, the trichomes or bristles rigid, appressed, deep brown, sometimes nearly black, at the base 1–6 cells wide, 1–3 cells thick, the apical cell elongate or globose. *Leaves* erect, 2.6–50.0 cm. long. *Petiole* subterete, plane or sulcate on the upper surface near the apex, castaneous or atropurpureous, rarely lighter, ca. 1/4 as long to equal the lamina, with sparse to dense pubescence, the trichomes rigid, clear, brown or bicolorous, the apical cell elongate or globose, sometimes glandular. *Lamina* elongate-triangular to linear, acuminate, the pinnae often longer in the lower half, 1–3-pinnate, usually 2-pinnate, 1.5–25 cm. long, 0.7–11.0 cm. wide, determinate, the apical bud minute. *Rachis* straight, sometimes subflexuous, the upper surface sulcate, the lamina tissue decurrent at least in the upper portion of the lamina, castaneous, with sparse to dense pubescence, usually more dense than on the petiole, the trichomes clear tan or brown, the apical cell usually elongate or globose, glandular. *Pinnae* at right angles to the rachis or slightly ascending, elongate-ovate or somewhat orbicular, the basiscopic side not or slightly larger, 0.2–10.0 cm. long, 0.2–3.0 cm. wide, herbaceous, sometimes rigid or coriaceous; *upper surface* pubescent, with erect, rigid, clear or yellowish trichomes, the apical cell usually elongate, sometimes globose; *lower surface* densely pubescent, the trichomes similar but denser than the upper surface; *stalk* 2–5 mm. long with ridges continuous with those of the rachis; *pinnules* orbicular or cuneate, usually with few large lobes, the margin shallowly crenate, plane or sometimes strongly incurved; *veins* terminating in a lobe short of the margin, usually slightly enlarged. *Border* differentiated into a yellowish rim, 2–5 cells broad, the cells elongate, projecting at the apical end, those at the segment apex about as long as broad or sometimes longer and protruding. *Sporangia* usually concentrated on the ultimate and penultimate veins and those of the next order near the rachis, the stalk short, of one or two tiers of clear cells, the annulus with 15–20 indurated cells. *Spores* tan or light brown, rarely darker, the proximal

face with few ridges, with a moderately broad equatorial flange, the angles slightly projecting, the distal face smooth or with a few, coarse tubercles.

A tendency for leaf dimorphism in *Eriosorus* is most pronounced in *E. hispidulus* as its fertile leaves are conspicuously larger than the sterile ones. This species is remarkable because of three distinctive characters: veins terminating short of the margins; a prominent marginal rim; and a rigid, erect leaf indument. These features not only readily characterize the species but often mark its involvement with other species. Several intermediate forms, showing the features mentioned, are treated following the main citations. Those from Antioquia, Colombia seem to involve *E. flexuosus*, although both this and *E. velleus* are reported from the same localities and the relationships may be more complex. Specimens designated by Klotzsch as *Gymnogramma Ottonis* may also relate to *E. flexuosus*, as indicated by the somewhat fractiflex rachises which are tan or lighter colored at the apex. Spores of these collections are abundant and seem to be well formed. These and other more coriaceous leaved specimens from northern Venezuela are best placed with *E. hispidulus* until their ecology and field relationships are known.

This species is closest to *Eriosorus hirtus* and the two are relatively more specialized than *E. myriophyllus* in their blackish rhizome bristles and light colored spores. Characters in *E. hispidulus*, such as the short vein ends and marginal rims, as well as the dimorphic leaves, represent a relatively more complex structure than *E. hirtus*. Their geographic ranges are also similar but the latter extends farther south in the Andes of Bolivia. *Eriosorus hispidulus* occurs in northern Colombia on Cerro La Horquita mountain and east to Mt. Roraima in British Guiana. The two Antillean records of the species are of geographic interest. Specimens from Puerto Rico are from El Yunque Peak and the species is known from nearby Two Peaks. The robust, glandular specimens collected by Howard and the one of Gastony from El Yunque are as large as some from Venezuela and indistinguishable from them. The Dominican collection is distinctive as indicated in the following key and discussion of var. *dominicensis*. The eglandular trichomes on the leaves of that variety represent a less specialized state and distinguish those plants from the glandular ones of var. *hispidulus* from the Greater Antilles and Guatemala.

KEY TO THE VARIETIES OF ERIOSORUS HISPIDULUS

Lamina elongate-triangular, the lower pinnae usually more than twice as long as broad; the upper half of the lamina mostly 2-pinnate; the base of the petiole with trichomes often with the terminal cell bulbous; spores tan, or light brown ..... 6a. *E. hispidulus* var. *hispidulus*.

Lamina linear, the pinnae about as long as broad, the lower pinnae as long as or slightly longer than broad; the upper half of the lamina mostly 1-pinnate; petiole trichomes with the terminal cell elongate; spores dark brown ..... 6b. *E. hispidulus* var. *dominicensis*.

6a. Eriosorus hispidulus var. hispidulus

FIG. 16A, MAP 7

Jamesonia hispidula Kze. Bot. Zeit. **2**:739. 1844. TYPE: *Moritz 72* (Kze. Farnk. **1**:196, t. 82, 1846)Venezuela, Caracas. This Moritz number was not found among his many collections studied in several European herbaria. The name is applied here from the original description and the illustration of this collection in the later work of Kunze.

Gymnogramma hispidula (Kze.) Kl. Linnaea **20**:407. 1847.

Gymnogramma Schomburgkiana Kze. ex Kl. Linnaea **20**:408. 1847. TYPE: *Schomburgk 1196*, British Guiana B! photo GH; isotype B! BM! G! photo GH, K!.

Anogramma Schomburgkiana (Kze. ex Kl.) Fée, Gen. Fil. 184. 1852.

Gymnogramma Ottonis Kze. ex Kl. Linnaea **20**:408. 1847. TYPE: *Otto 630*, Venezuela, "auf den nordlichen Cordillera von Venezuela, Anden 7000 f." B! photo GH; isotype: BM! G! K! NY-frag!.

Annogramma Ottonis (Kze. ex Kl.) Fée, Gen. Fil. 185. 1852.

Psilogramme hispidula (Kze.) Kuhn, Fests. 50 Jub. Reals Berl. (Chaetop.) 341. 1882.

Psilogramme Schomburgkiana (Kze. ex Kl.) Kuhn, op. cit. 341. 1882.

Psilogramme Ottonis (Kze. ex Kl.) Kuhn, op. cit. 340. 1882.

Psilogramme portoricensis Maxon, Contrib. U.S. Nat. Herb. **17**. 412, t. 15, 1914. TYPE: *Brother Hioram 348*, Puerto Rico, El Yunque, 1110 m., March 1912 US!

Gymnogramma portoricensis (Maxon) C. Chr. Ind. Suppl. Prélim. 19. 1917.

Eriosorus Schomburgkianus (Kze. ex Kl.) Copel. Gen. Fil. 58. 1947.

Eriosorus Ottonis (Kze. ex Kl.) Vareschi, Fl. Venez. **1**(2):638. 1969.

Lamina elongate-triangular, 0.7–11.0 cm. wide, the lower pinnae usually twice as long as broad, the upper half of the lamina mostly 2-pinnate. *Rachis* sparse to densely pubescent, the trichomes with the apical cell elongate or globose, sometimes glandular. *Spores* tan or light brown.

A few variants and hybrids with *Jamesonia* are treated following the main citations. Variants from the Department of Antioquia, Colombia, are difficult to interpret as *Eriosorus hispidulus* occurs there with both *E. flexuosus* and *E. velleus*. The hybrids are likewise complex and involve more than one species of *Jamesonia*.

Terrestrial, in subalpine forest, at base of large boulders, on bluffs or ledges, 1800–2865 m., Guatemala, Puerto Rico, northern Colombia east to British Guiana.

ADDITIONAL SPECIMENS EXAMINED: **Guatemala. Chiquimula:** se. of Concepción de las Minas, *Steyermark 30990* (F, US). **Colombia. Magdalena:**

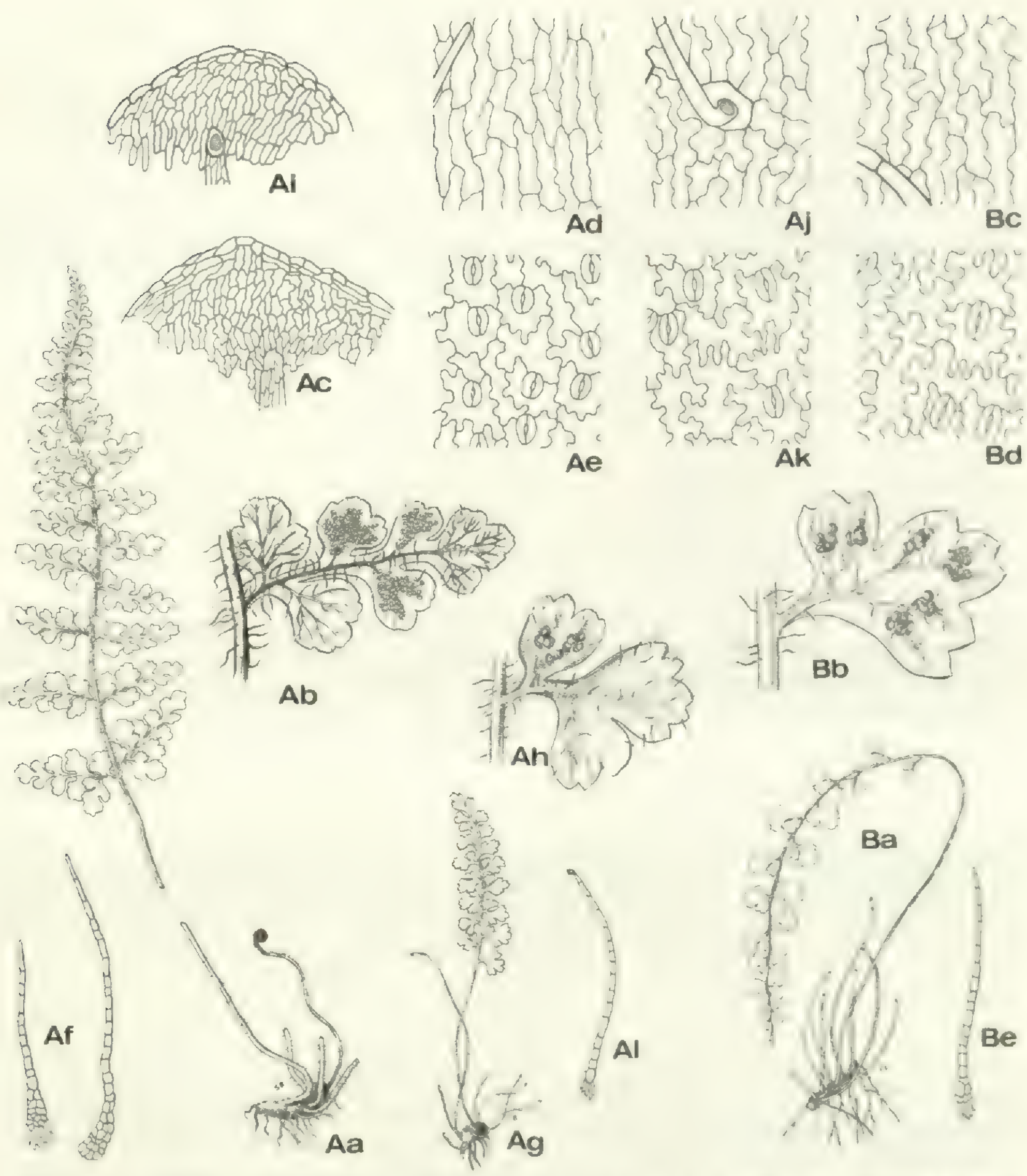


FIG. 16. *Eriosorus hispiduus*. Aa–Al var. *hispidulus:* Aa, habit with central half of the petiole omitted, × 1/3; Ab, pinna and portion of the rachis, × 1–1/3; Ac, margin with vein ending below, × 20; Ad–Ae, epidermis, × 40, Ad upper surface, Ae lower surface, all from *Alston & Williams 295,* Venezuela (GH); Af, rhizome bristles, × 10, *Pittier 6236* (US); Ag, habit of small plant, × 1/3; Ah, pinna and portion of the rachis, × 2; Ai, margin with vein below darker basal cell of trichome, × 20; Aj–Ak, epidermis, × 40, Aj upper surface, Ak lower surface; Al, rhizome trichome, × 10, all from *Howard 15635,* Puerto Rico (A). Ba–Be, var. *dominicensis:* Ba, habit, × 1/3; Bb, pinna with portion of the rachis, × 2; Bc–Bd, epidermis, × 40, Bc upper surface, Bd lower surface; Be, rhizome bristle with longer cells from rhizome epidermis, × 10, all from *Chambers 2591* Dominica (GH).

top of Horqueta Mt. *H. S. Smith 2591* (BM, F, GH, K, NY, P, S-PA, US). **Norte de Santander:** Ocaña, *Kalbreyer 476* (B, K). **Antioquia:** Medellín, *Charetier 2* (US); *Henri-Stanislas 1651* (US). **Venezuela.** *Birschel,* 1855 (BM). **Distrito Federal:** Los Venados, *Allart 108,* in part (US); Galipán, *Funck & Schlim 290* (BM, GH, HBG, K, P, W), *300* (B, BM, G-K-in part, W); *Linden 290* (B); Cerro Avila, *Steyermark 55639* (F, GH, US); Galipán, *Tamayo 109*

(VEN); Avila, *Vogel 58* (F-in part, US); between Los Flores & Boca del Tigre, *Williams 10922* (F-in part, VEN), *Williams & Alston* 295, (BM, GH). **Miranda:** Fila del Naiguatá, *Pannier* 99 (VEN); Pico de Naiguatá, *Pittier 6236* (B, US-601971); *Steyermark 63015* (F, GH-NY-in part, US). **Aragua:** Colonia Tovar, *Fendler* 1856–57 (B), 359 (K); Gran Sabana, *Maguire* 33513 (US); Sorotopán-Tepuí, *Steyermark 60109* (F, NY, US), Roraima, *58714* (F, US), Chimantá Massif, *75820* (F, VEN), *Steyermark & Wurdack 719* (VEN). **Mérida:** *Moritz 96* (B, GH, HBG, K, P). **British Guiana.** *Appun (Glaziou 12363)* (B, C, NY-frag., P), Roraima, *Appun 1091* (K); slopes below Roraima, *Jenman*, 1894 (E, NY); upper slope, Roraima, *im Thurn 164* (BM, K, NY-frag., US, W). **Puerto Rico:** Luquillo Mts., El Yunque, *Britton & Bruner 7633* (NY, US); *Gastony 11* (GH); *Howard 15635, 15697* (A); *Sargent 315* (US); *Sintenis 1785* (B, P, US); *Tryon & Tryon 7084* (GH).

VARIANTS INVOLVING ERIOSORUS HISPIDULUS VAR. HISPIDULUS

1. The following variant collections have aborted or irregular spores, flexuose rachises and seem to represent forms intermediate between *Eriosorus hispidulus* and *E. flexuosus*. They occur in areas where both species have been collected and resemble the latter in the strongly flexuosus and light colored rachises. They are included under *E. hispidulus* on the basis of erect leaves with broad, cuneate ultimate segments and veins ending short of the margin. The Lehmann collection consists of several variable leaves, possibly from more than one rhizome and represents a population sample of variants intermediate to these species. The other collections from Antioquia are similar but may possibly involve *E. velleus* which also occurs in the department. The collections from Pico de Naiguatá have especially reduced, nearly 1-pinnate leaves and strongly resemble *Jamesonia*. **Colombia. Magdalena:** Sierra Nevada de Santa Marta, *Barclay & Juajibioy 6540, 6548, 6916* (GH); *Bolinder*, 1921 (BM, C, S-PA). **Antioquia:** near Medellín, *Charetier 34*, in part (US), Laguna de Guarne, *Daniel 666* (US), Carretera a San Pedro, *1233* (US-in part); Yarumal, *Lehmann 7257* (B, F, GH, K, P, US). **Venezuela. Miranda:** Pico de Naiguatá, *Pittier 6236* (US-694143 in part); *Steyermark 63015* (F, GH-NY-in part, US). **British Guiana:** Roraima, *Jenman*, 1897 (NY); *im Thurn 197* (BM, K, US).

2. The collection cited below is included under this species because it will key out here on the veins ending short of the margins. The strong rims bordering the ultimate segments in these specimens are also characteristic of the species. This variant differs from the previous one and from other material included under the species in having a strong deltoid shape and 3-pinnate lamina. The spores are highly irregular. The collection possibly represents an intermediate involving *E. hirtus*, which has broader, more compound leaves. **Colombia. Santander:** Río Frio, *Kalbreyer 1954* (B, K), *1954a* (B).

PUTATIVE HYBRIDS INVOLVING ERIOSORUS HISPIDULUS var. HISPIDULUS

E. hispidulus var. hispidulus × Jamesonia

Gymnogramma incisa Mart. & Linden ex Kze. Farnk **2**:78, t. 132. 1851. TYPE: *Linden 1044*, Colombia, Prov. Mariquita, Quindiu, inter Palmilla et

Las Tapis, Herb. Mart. BR photo GH; isotypes: BM!, BR photo GH, G!, GH!, K! photos GH, P! photo GH, S-PA!, W!.

Psilogramme incisa (Mart. & Linden ex Kze.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 336. 1882.

The Linden collection has pinnae exceptionally variable in size and shape and the spores appear well developed but have irregular sculpture. The pronounced rims bordering the pinnae and short vein ends show a relation to *Eriosorus hispidulus* and the compact pinnae and attenuated 1-pinnate apex of the lamina resemble *Jamesonia*. The Lindig collection is similar and has aborted sporangia. These collections have a marked resemblance to *E. velleus*, as noted under that species. **Colombia. Cundinamarca:** Fusagasuga, *Lindig 76* (P).

Two other collections have largely aborted sporangia and few, very irregular spores. The leaves are mostly 1-pinnate. The pinnae are similar to those of the previous hybrid which resembles *E. hispidulus*. It is possible that several species of *Jamesonia* are involved in these hybrids which are from different geographic areas. The collection from Honduras is from the lower part of a cloud forest. I have seen no other record of either *Eriosorus* or *Jamesonia* from this cerro, but another collection from the same department is given under *E. hirtus*. **Honduras. Morazán:** Cerro de Uyuca, 5500–5740 ft. *M. J. Howard 51* (US). **Venezuela. Mérida:** on bank at margin of forest, *Alston 5781* (BM, GH).

6b. **Eriosorus hispidulus** var. **dominicensis** A. F. Tryon, var. nov.

FIG. 16B, MAP 7

Lamina elongato-linearis in dimidio superiore plerumque 1-pinnata, pinnae 1.5–2.0 cm. latae longitudine latitudem aequantes, rachis sparse vel modice pubescens trichomatibus cellula elongata eglandulata terminali praeditis, sporae atrofuscae.

TYPE: Dominica, West Indies, summit of Morne Trois Pitons. In pendent mosses, on exposed rock, in pygmy forest, ca. 4400 f., Jan. 17, 1966, *K. L. Chambers 2596* GH; isotype: OSC, US.

Lamina linear-elongate, the pinnae about as long as broad, 1.5–2.0 cm. wide, the upper half of the lamina mostly 1-pinnate. *Rachis* sparsely to moderately pubescent, the trichomes with the apical (terminal) cell elongate. *Spores* deep brown.

The veins ending short of the margin, the prominent marginal rim and rigid lamina trichomes show that this collection is related to others of *Eriosorus hispidulus*. It is distinguished from them by having a linear and 1-pinnate lamina. The well developed leaves, 18–23 cm., are longer than but not as broad as most Puerto Rican specimens. The bristle-like eglandular trichomes on the lamina and rhizome (Fig. 16Be) also distinguish this variety from that of Puerto Rico, and show a resemblance to the eglandular populations of var. *hispidulus* of Colombia and northern Venezuela. The different trichomes in the two Antillean populations suggest that they have different South American origins.

7. **Eriosorus velleus** (Baker) A. F. Tryon, comb. nov.

Fig. 17, Map 8

Gymnogramma vellea Bak. Jour. Bot. Brit. & Foreign **19**:206. 1881 (not *G. vella* Kuhn, Fil. Afr. 61. 1868). TYPE: *Kalbreyer 1487,* Colombia: Antioquia in 1879, K! photo GH, NY-frag.; isotypes: B! BM! photo GH.

Gymnogramma hirtipes C. H. Wright, Kew Bull. No. **2**:61. 1907. TYPE: *R. B. White,* Colombia K! photo GH, US-frag!

Gymnogramma antioquiana Rosenst. Mém. Soc. Neuchâtel. **5**:54. 1912. TYPE: *Mayor* 82, Colombia, Antioquia, Alto L. Miquel, S-PA! photo BM, GH; isotypes: P! photo GH, US! photo GH.

Rhizome repent, usually with short internodes, ca. 3–5 mm. in diameter with trichomes or bristles crispate or rigid, appressed, lustrous, ruddy brown, at the base 1–4 cells wide, 1 or 2 cells thick, the apical cell elongate or globose. *Leaves* erect, 10–40 cm. long. *Petiole* plane or slightly channeled on the upper surface near the rhizome, channeled at the apex, atropurpureous, equal to or three times longer than the lamina, with sparse to dense pubescence, the trichomes rigid, clear to light brown, often bicolorous, the apical cell elongate or globose. *Lamina* elongate-triangular or somewhat lanceolate with acuminate apex, the basal pinnae usually longest, 2-pinnate, 5–24 cm. long, 1.5–5.0 cm. wide, determinate, the apical bud minute. *Rachis* straight, the upper surface channeled, the lamina decurrent except near the base, atropurpureous to castaneous, densely pubescent, the trichomes clear or light brown, the apical cell elongate or globose, glandular. *Pinnae* slightly ascending, the basal ones more strongly so, lanceolate, equilateral, 1.0–3.5 cm. long, 0.4–1.5 cm. wide, rigid herbaceous, subsessile; *upper surface* sparsely to densely pubescent, the trichomes clear or tan, the apical cell usually elongate; *lower surface* with similar, usually denser, trichomes; *stalk* 1–3 mm., usually with decurrent lamina tissue; *pinnules* cuneate, the *ultimate segments* often bilobate, the margins usually retuse, plane; *veins* terminating in a sinus at or near the margin, not or slightly enlarged (usually obscure on the lower surface); *border* usually undifferentiated, or narrow with a row of elongate cells. *Sporangia* most abundant on the penultimate and basal portion of ultimate veins, the stalk of one or two tiers of cells subtended by a cushion of clear or brown cells (the capsules may be closely placed with 1–5 per cushion), the annulus of 15–21 indurated cells. *Spores* deep brown, the proximal face with tubercles adjacent to and more prominent than the triradiate scar, with a broad, often irregular equatorial flange, the angles not projecting, the distal face with numerous tubercles, sometimes aborted.

This species is unusual in having leaves with a slender lamina and equilateral pinnae, and also because its geographic range is restricted to the department of Antioquia, Colombia. The frequently aborted and peculiarly sculptured spores indicate irregularities in the specimens. The collections treated as putative hybrids with *Jamesonia* under *Eriosorus hispidulus* (*Lindig 76,* from Fusagasuga) and the Linden collection typifying *Gymnogramma incisa,* may possibly be related to *E. velleus*. The hybrids have similar but broader leaves than *E. velleus*. They occur in the Cordillera Oriental, east of Antioquia.

On banks along the margins of forests, in shade along forest border or on moist banks near streams. Department of Antioquia, Colombia, at 1560–3000 m.

ADDITIONAL SPECIMENS EXAMINED: **Colombia.** *Schmidtchen,* 1879 (K). **Antioquia:** Santa Elena, *Archer 1184* (US); *Daniel 965* (COL, F, US), El Santuario, *549* (US), carretera a San Pedro, *1233*-in part (US); Copacabana, *Henri-Stanislas 1664* (US), near Medellín, *Sarmiento,* Oct. 1945 (GH); ca. Las Palmas, *Hodge 6732* (GH, US); Yarumal, *Tomás 4441* (US).

8. **Eriosorus Warscewiczii** (Mett.) Copel. Ind. Fil. 59. 1947

FIG. 18, MAP 10

Gymnogramma Warscewiczii Mett. Ann. Sci. Nat. V,2:211. 1864. TYPE: *Warscewicz 20,* Costa Rica, Cartago, Vulcán, Herb. Mett. B! photo GH; isotypes: B! frag. NY! P!

Psilogramme Warscewiczii (Mett.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 337. 1882.

Rhizome elongate repent, with long internodes, ca. 2–4 mm. in diameter, the trichomes or bristles crispate or rigid, appressed, golden to ruddy brown, at the base usually one or two cells, the apical cell elongate. *Leaves* erect, 10–80 cm. long. *Petiole* plane or somewhat channeled on the upper surface near the rhizome, strongly channeled at the apex, castaneous or darker near the rhizome, equal to or up to two times longer than the lamina, with sparse crispate, light brown or tan trichomes, the apical cell elongate. *Lamina* elongate-triangular or -rhomboid, acuminate, usually 3-pinnate, 5–40 cm. long, 2–9 cm. wide, determinate, the apical bud small, somewhat pubescent. *Rachis* straight or slightly flexuose, the upper surface channeled, the lamina decurrent at the apex and pinnae axils, castaneous to atropurpureous, sparsely to moderately pubescent, the trichomes clear to light brown, the apical cell elongate. *Pinnae* slightly ascending, elongate-deltoid, equilateral, or the basiscopic side slightly larger, 0.5–5.5 cm. long, 0.2–4.0 cm. wide, rigid-herbaceous to coriaceous; *upper surface* glabrous; *lower surface* sparsely to moderately pubescent, the trichomes clear, the apical cell elongate, or globose; *stalk* 2.5–10.0 mm. long, with ridges continuous with those of the rachis; *pinnules* elongate-triangular, deltoid or ovate, the *ultimate segments* cuneate, with few, shallow or somewhat bifid lobes, the margins strongly cleft, usually incurved; *veins* terminating in a sinus at the segment margin, clavate or subclavate; *border* with 1–3 rows of elongate cells up to 4 times longer than broad. *Sporangia* more abundant on the penultimate veins, extending nearly to the costa, the stalk usually of one tier subtended by a cushion of brown cells, the annulus of 18–21 indurated cells. *Spores* deep brown, the proximal face with broad ridges parallel to the triradiate scar, with a narrow equatorial flange, the angles not projecting, the distal face with few large tubercles and smaller papillae.

Field work in Costa Rica has provided a new concept of variation in *Eriosorus Warscewiczii* involving hybridization with species in this genus and others with grossly different morphological form in *Jamesonia.* On Volcán Poás, it occurs in isolated

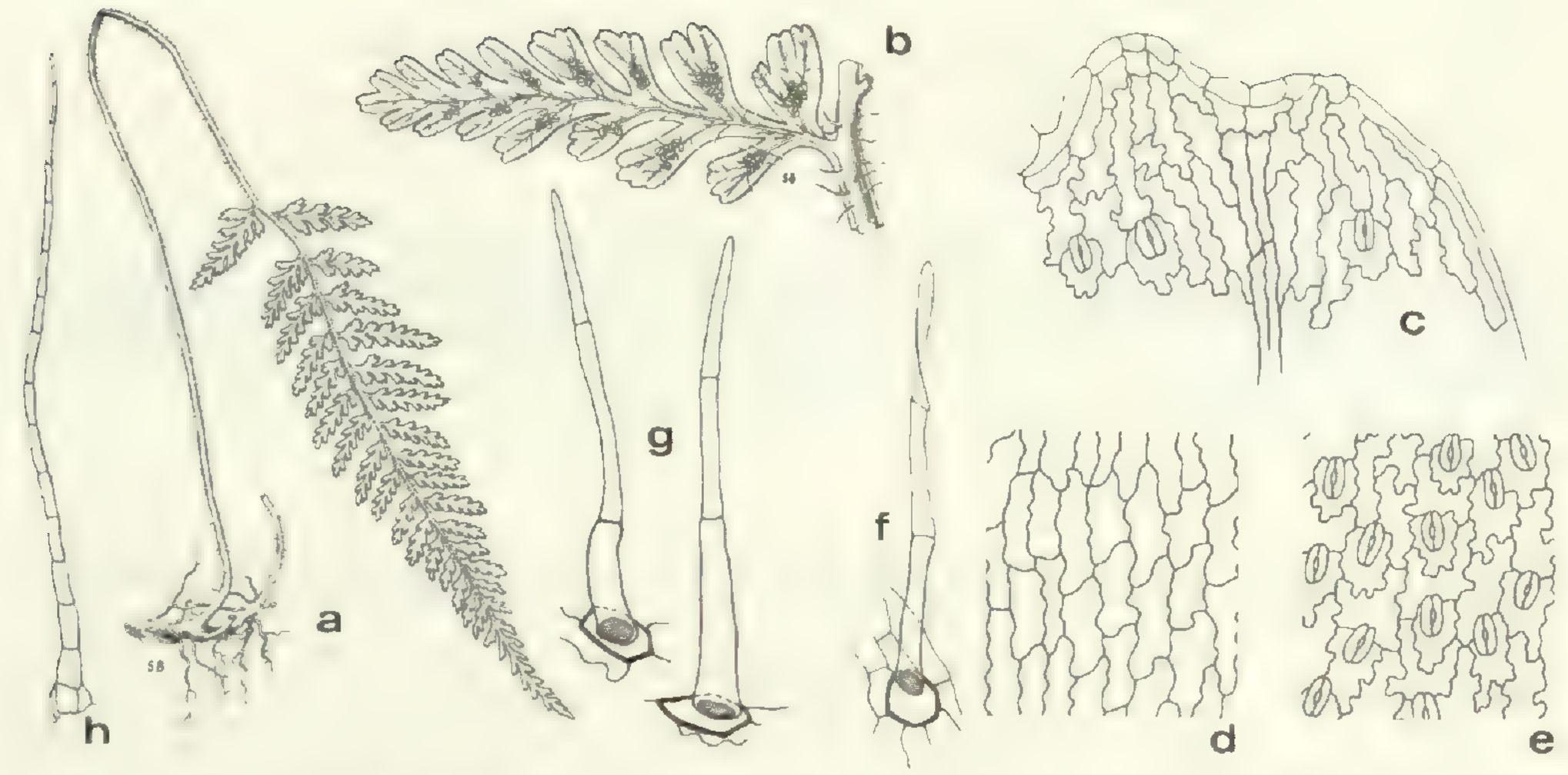


FIG. 17. *Eriosorus velleus*: a, habit, × 1/3; b, pinna, × 1–1/3; c, margin with vein end, × 10; d, upper epidermis; e, lower epidermis; f–g, lamina trichomes, f upper surface, g lower surface, all × 40, from *Hodge 6732* (GH); h, rhizome bristle, × 20, *Daniel 549* (US).

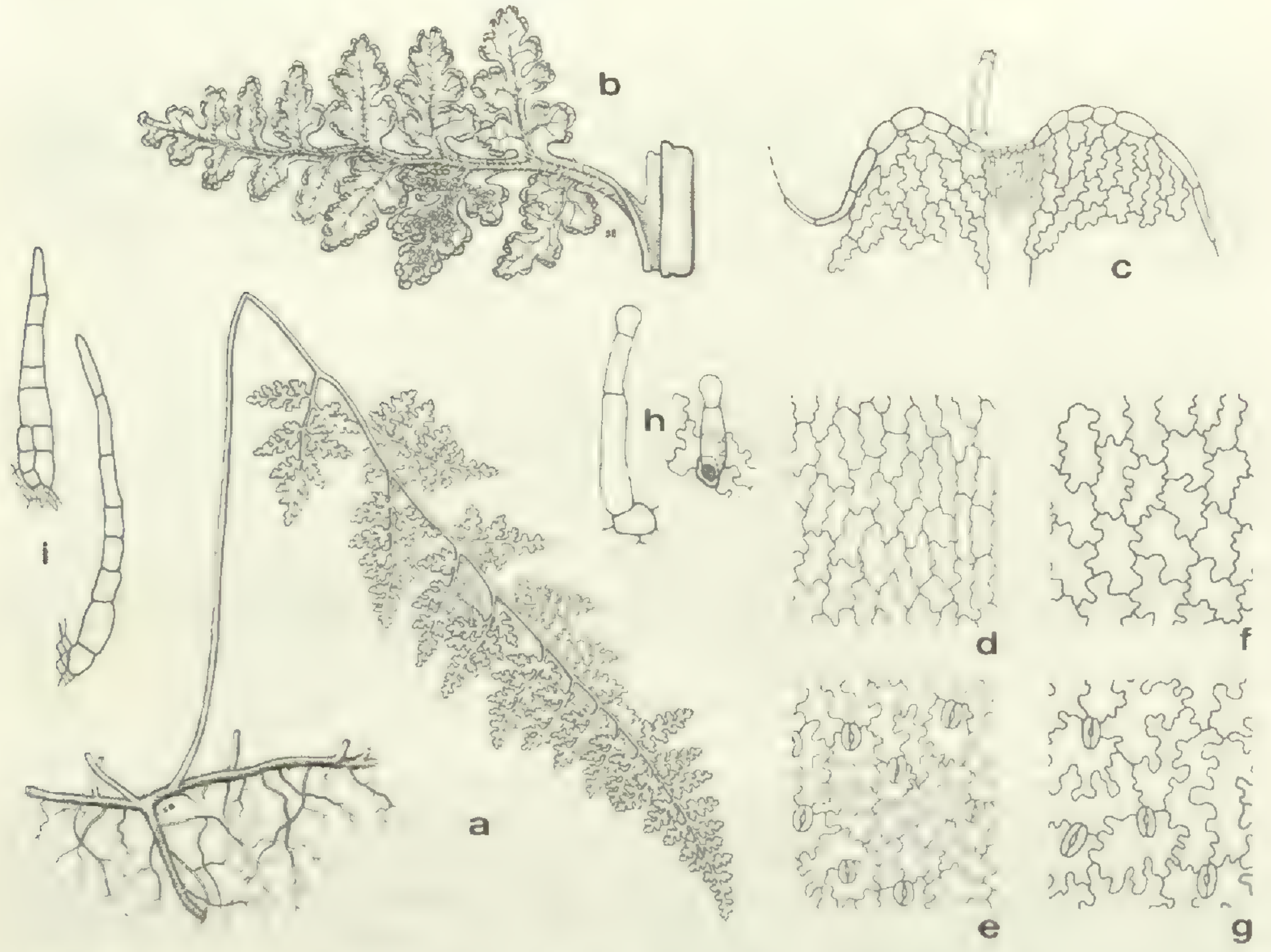


FIG. 18. *Eriosorus Warscewiczii*: a, habit, × 1/3; b, pinna lower surface with a portion of the channeled upper surface of the rachis, × 1–1/3, both from *Tryon & Tryon 7003* (GH); c, margin with vein end and trichome from lower surface, × 34; d–g, epidermis, × 40, d upper surface, e lower surface, all from *Tryon & Tryon 7050*, Costa Rica (GH); f upper surface, g lower surface, *Tryon & Tryon 5979*, Colombia (GH); h, trichomes, lower pinna surface, × 40, *Tryon & Tryon 7050* (GH); i, rhizome trichomes with smaller cells of epidermis, × 20, *Tryon & Tryon 7009* (GH).

colonies at highest altitudes near the summit and around the crater. Somewhat lower, it grows intertwined among shrubs with *E. flexuosus*. The latter is especially abundant here growing upon slash and litter in deforested areas. The hybrids, treated under *E. flexuosus* because of a marked resemblance to that species, are vigorous and sporiferous but with irregular spores. *Eriosorus Warscewiczii* also occurs with *Jamesonia Scammanae* on Cerro de la Muerte, in the Cordillera de Talamanca. There are frequent hybrids, found where these grow together, that somewhat resemble the Andean species *E. cheilanthoides*. A collection of the hybrid from Chirripo Grande, some distance from the cerro, was earlier described as *Gymnogramma Kupperi*.

Cytological samples of *Eriosorus Warscewiczii* from Poás and from Cerro, consistently have 87 bivalents at meiosis, while both of the hybrids involving the species have ca. 174 largely univalents and a few multivalents. Spores of the hybrid plants are presumed to be sterile since they are irregular and could not be germinated. A chromosome number of 87 for *E. Warscewiczii* is interpreted as representing the hexaploid level and is indicative of a complex history, aside from complications of the current hybridization.

Eriosorus Warscewiczii is known primarily from Costa Rica but a collection is included from southern Colombia. It connects the Costa Rican plants with those of Colombia and ties the species with the geographic center of the genus in South America. The epidermal cell patterns, shown in Fig. 18 f, g, from the Colombian specimens, have larger cells and in the upper epidermis more strongly undulate walls. This collection is identified with those from Costa Rica because of similarities of the rhizome, such as the elongated internodes which have simple, light brown trichomes, cuneate vein ends, unspecialized borders on the ultimate segments, and deep brown spores. The relationship of *E. Warscewiczii* appears to be closer to the Colombian species *E. novogranatensis*, with which it occurs in the Department of Cauca, than to any of the Costa Rican species.

On banks along trails and crevices among rocks at summits of volcanos and mountains in Costa Rica and Colombia, at 2300–3400 m.

ADDITIONAL SPECIMENS EXAMINED: **Costa Rica.** *Pittier 12* (K, NY-frag., ex K). **Heredia:** slopes of Barba, *Lent 53* (GH). **Alajuela:** Volcán Poás, *Alfonso Jiménez 452* (F), *3950* (F, GH); laguna del Poás, *Quirós 693* (F);

J. D. Smith 6930 (B, BM, GH, K); *Standley* 34869 (MICH); *Tonduz* 10712 (G, P, W); at crater, 2525 m. *Tryon & Tryon* 7000, along road below crater, 2500 m., *7003, 7009, 7017*. **Cartago:** Volcán de Turrialba. *Pittier* 7488, Herb. Nac. C.R. 13256 (B, BM, GH, K, P); Volcán Irazú, *P. A. Allen* 701 (GH); *Carlson* 3544 (F); *Hatch* 182 (F); *Orsted* 49 (C); *Pittier* 160, 1061 (G, P); *Quirós* 822 (F); *R. L. Rodriguez* 319 (GH); *Scamman* 6070, 6071, 6073 (GH); *Stork* 1289, 2013 (MICH); *Weber* 6020 (GH); *Williams & Molina* 13907 (F, GH); *Williams & Williams* 24081 (F); Cerro de la Muerte, *Scamman* 6072 (GH); *Tryon & Tryon* 7050 (GH). **Colombia. Cauca:** Páramo de Puracé, *Tryon & Tryon* 5979 (GH).

PUTATIVE HYBRID INVOLVING ERIOSORUS WARSCEWICZII

Eriosorus Warscewiczii × Jamesonia Scammanae

Gymnogramma Kupperi Losch, Mitt. Bot. Staatssam. 1:21. 1950. TYPE: *W. Kupper* 1223, Costa Rica, Cartago, Chirripo Grande, 3500 m. M! photos BM, GH. **Costa Rica. Cartago:** Cerro Asuncíon, *A. Jiménez* 3387 (F, GH); Cerro de la Muerte, *Tryon & Tryon 7048, 7049* (GH).

9. **Eriosorus novogranatensis** A. F. Tryon, spec. nov.

FIG. 19, MAP 9

Rhizoma internodiis longis trichomatibus pallide fuscis ad basim cellulis plerumque 2 vel 1 latis, lamina elongato-triangularis 1- vel 2-pinnata apice indeterminato gemma grandi tomentosa, rhachis recta castanea tomentosa vel plerumque minus dense pubescens, pinnae elongato-triangularis vel deltoideae rigido-herbaceae vel coriaceae, pinnulae ovatae adaxialiter glabrae abaxialiter sparsim pubescentes, nervi ad sinum marginis attingentes extremis clavatis, sporae atrofuscae.

TYPE: Colombia, Tolima, Boquerón de Quindiu, 3400 m. *A. H. G. Alston* 7728, GH; isotype: BM.

Rhizome elongate repent with long internodes, ca. 2–4 mm. in diameter, the trichomes crispate, golden brown, at the base usually one or two cells, the apical cell elongate. *Leaves* erect, 10–88 cm. long. *Petiole* upper surface plane or somewhat channeled near the rhizome, strongly channeled at the apex, castáneous to atropurpureous, about half as long as to equal the length of the lamina, with dense, matted tomentum, the trichomes crispate, tan or bicolorous, the apex sometimes darker, the apical cell somewhat elongate. *Lamina* elongate-triangular or -rhomboid, acuminate, usually 3–pinnate, 18–56 cm. long, 4–13 cm. wide, determinate, the apical bud usually large, tomentose. *Rachis* straight, the upper surface channeled, the lamina decurrent at axils of pinna rachises, the lower surface convex, castaneous, usually densely pubescent or tomentose, the trichomes tan, the apical cell elongate. *Pinnae* slightly ascending, elongate-triangular to deltoid, the basiscopic side slightly larger, 0.2–8.5 cm. long, 1.5–3.5 cm. wide, rigid herbaceous to coriaceous; *upper surface* glabrous; *lower surface* sparsely pubescent, mainly along the veins, the trichomes clear or tan, crispate, the apical cell elongate; *stalk* 2–10 mm. long with ridges continuous with those of the rachis; *pinnules* elongate-ovate or deltoid, the *ultimate segments* ovate or orbicular with margins crenate or with few, larger lobes, sometimes incurved; *veins* terminating in a sinus at or slightly short of the margin,

clavate; *border* with 1–3 rows of elongate cells up to 10 times longer than broad. *Sporangia* along the veins most abundant on the penultimate veins, the stalk with two or three tiers of clear cells, often subtended by a cushion, the annulus of 17–21 indurated cells. *Spores* deep brown, the proximal face with strong ridges or tubercles adjacent to the triradiate scar, with a moderately broad equatorial flange; the angles not or slightly projecting, the distal face with few, large tubercles.

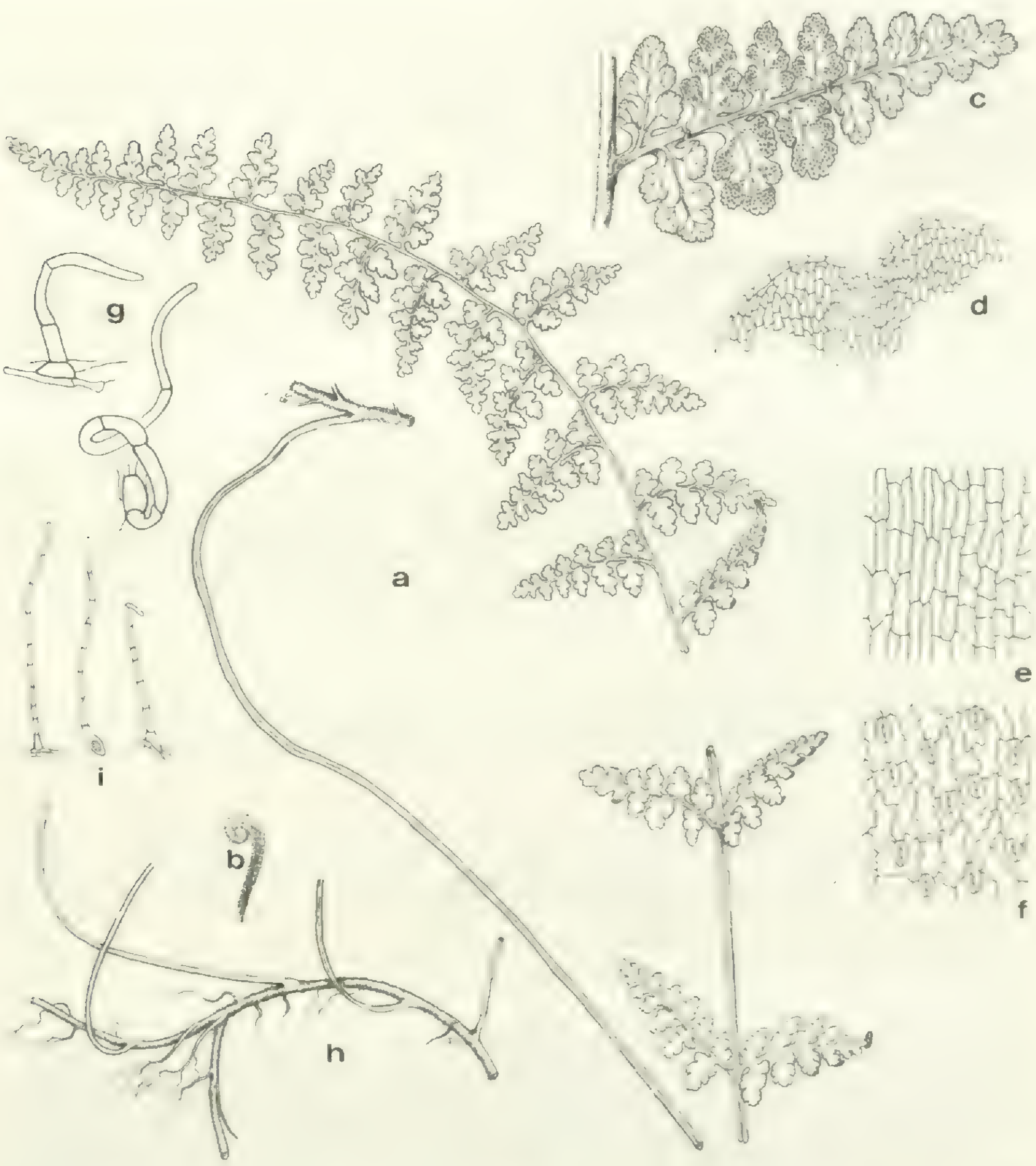


FIG. 19. ***Eriosorus novogranatensis:*** **a, habit, the leaf with 3 pairs of central pinnae and upper portion of petiole omitted, × 1/3; b, leaf bud with dense tomentum, × 1/3, *Cuatrecasas 18851* (GH); *c*, pinna with sporangia on central pinnules, × 2/3; d, margin with vein end, × 20; e, upper epidermis; f, lower epidermis; g, trichomes, lower pinna surface, all × 40; h, portion of branching rhizome with 4 petiole bases, × 1/3; i, rhizome trichomes, × 10, all from *Alston 7728* (GH).**

This distinctive species has a broad distribution in Colombia, ranging from the Ecuadorian border northward, mainly along the Cordillera Oriental nearly to the Venezuelan frontier. The long internodes and simple trichomes on the rhizome distinguish it from other Colombian species and show a closer alliance to *Eriosorus Warscewiczii.*

On steep mossy bank or forest border, Colombia, at 2745–3400 m.

ADDITIONAL SPECIMENS EXAMINED: **Colombia. Norte de Santander:** Sisacita, Ocaña to Pamplona, 9000 ft., July 1879, *Kalbreyer 1107* (K), at 9200 ft. *1110* (B, K). **Santander:** Bucaramanga, road to Cucuta, *Sandeman 6034* (K). **Cundinamarca:** Between Bogotá and Honda, *Stübel 432* (B). **Cauca:** Alto del Duende, *Cuatrecasas 18851* (A, F, GH, US). **Narino:** Cocha-Patascoy, *Stübel 240* (B). **Meta:** Lanos de San Martin, *Stübel 682* (B).

VARIANT INVOLVING ERIOSORUS NOVOGRANATENSIS

The variant collection of Lindig, treated below, consists of a large suite of ample specimens from two different localities. The two distinct morphological forms in this collection unfortunately cannot be associated with the localities: one with elongate-triangular leaves and pinnae has dense, capitate glands on the lamina; the other, with deltoid lamina and pinnae, has sparse, glandless trichomes. The second resembles *Eriosorus Warscewiczii* and undoubtedly accounts for the inclusion of this collection among those cited with the original description of that species. This collection seems best placed here but resembles *E. Warscewiczii* indicating a close relationship with it. The collection of *E. Warscewiczii* from Colombia, as well as these intermediate specimens, suggests the possibility that the latter may be derived from *E. novogranatensis.*

Colombia. Cundinamarca: Páramo San Fortunato, 2800 m., *Lindig 299* (B, BM); Monserrate, Bogotá, 3200 m., *Lindig 299* (BM, GH, K, P).

10. **Eriosorus rufescens** (Fée) A. F. Tryon, Rhodora **65**:56. 1963

FIG. 20, MAP 11

Gymnogramma rufescens Fée, Gen. Fil. 181, t. 19C, f. 3. 1852. TYPE: *Mathews,* Peru, Andes. The illustration which shows a small leaf is taken to represent the name. The description includes dimensions of a larger leaf and suggests that the Mattews collection of Fée may be the same as that typifying *G. Mathewsii,* which consists of small plants and large leaf fragments.

Gymnogramma mohriaeformis Kunze ex Mett. Fil. Lechlerianae 1:9. 1856. LECTOTYPE: *Lechler 2255,* Peru, San Gavan, in 1854, Herb. Kze. B! photo GH; isolectotypes: Herb. Mett. B! photo GH! BM! photo GH, E!, G! photo GH, GH! K!, frag. NY!, P! photo GH, S-PA!, W! The specimen in Herb. Kunze with his determination and with a descriptive note by Mettenius is taken as the most authentic among the specimens of this widely distributed collection.

Gymnogramma Mathewsii Hook. Sp. Fil. **5**:128. 1864. TYPE: *Mathews 1814,* Peru, 1835 K! photo GH; isotypes: B!, BM!, E!, G!, K!, frag. NY!, P!

Psilogramme rufescens (Fée) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 336. 1882.

Psilogramme Mathewsii (Hook.) Kuhn, op. cit. 337. 1882.

Eriosorus Mathewsii (Hook.) Crabbe, Brit. Fern Gaz. 9:314. 1967.

Rhizome repent, the internodes short, ca. 2–3 mm. in diameter, with rigid, appressed trichomes or bristles, deep brown to black, at the base 1–3 cells, the apical cell usually elongate or globose. *Leaves* erect, 10–50 cm. long. *Petiole* subterete, somewhat channeled near the lamina, atropurpureous, usually twice as long as the lamina, with sparse to dense pubescence, the trichomes usually rigid, erect, tan, brown or bicolorous, the apical cell elongate or globose. *Lamina* elongate-triangular, the apex acuminate, 2-pinnate, 3–30 cm. long, 2.5–10.0 cm. wide, determinate, the apical bud small. *Rachis* straight, the upper surface shallowly channeled near the lamina, decurrent at the apex, atropurpureous, usually lustrous, moderately to densely pubescent, the trichomes ruddy brown or bicolorous and lighter at the base, the apical cell elongate, also some shorter, tan trichomes with the apical cell globose. *Pinnae* at right angles to the rachis, deltoid, elongate-triangular or ovate with an obtuse apex, the basiscopic side sometimes slightly larger, 1.0–5.5 cm. long, 0.5–3.3 cm. wide, rigid herbaceous to coriaceous; *upper surface* moderately pubescent, the trichomes clear, tan or bicolorous, the apical cell elongate or globose; *lower surface* more densely pubescent along the veins, the trichomes tan, or deep brown with a clear base, those on the veins mostly longer, the apical cell elongate, or globose, glandular; *stalk* on lower pinnae up to 3 mm., those above more or less decurrent; *pinnules* usually ovate, shallowly lobed, the margins crenate or more deeply cleft, plane; *veins* terminating at the margin, usually broadly clavate; *border* narrow, 1–3 rows of slightly elongated cells, at the vein end shorter, with rigid trichomes. *Sporangia* mostly on the penultimate veins and next order toward the rachis, the stalk of one or two cells subtended by a cushion of brown cells also with trichomes, the annulus of 15–24 indurated cells. *Spores* deep to usually golden brown, the proximal face with broad ridges adjacent to the triradiate scar, with a broad equatorial flange usually slightly irregular, the three angles not or slightly projecting, the distal face with few to many tubercles, sometimes aborted.

I have found no collections bearing the annotation of Fée which would unequivocally establish the application of his name. His specimen was probably the same as that typifying Hooker's *Gymnogramma Mathewsii*, based on *Mathews 1814*, which consists of small, complete, sparingly fertile plants and fragments from at least two large leaves which agree with Fée's description of *G. rufescens*. The smaller plants are also similar to the Lechler collections representing the type series of *G. mohriaeformis*. The epidermal cell patterns from these types shown in Fig. 20 are similar.

This is one of the more advanced species at the intermediate level of specialization shown in Fig. 1. It occurs at high altitudes in the Andes and relationships can be readily established with *Eriosorus setulosus* and *E. longipetiolatus* which are more special-

Map 10–12. Map 10, ***Eriosorus Warscewiczii,*** **dot; hybrid,** ***E. Warscewiczii*** × *E. flexuosus* var. *flexuosus,* rhomb.; hybrid, *E. Warscewiczii* × *Jamesonia Scammanae,* star. Map 11, *E. rufescens,* dot; variant, circle; *E. setulosus,* rhomb.; *E. longipetiolatus,* star. Map 12, *E. aureonitens,* dot; *E. accrescens,* rhomb.; *E. Stuebelii,* star.

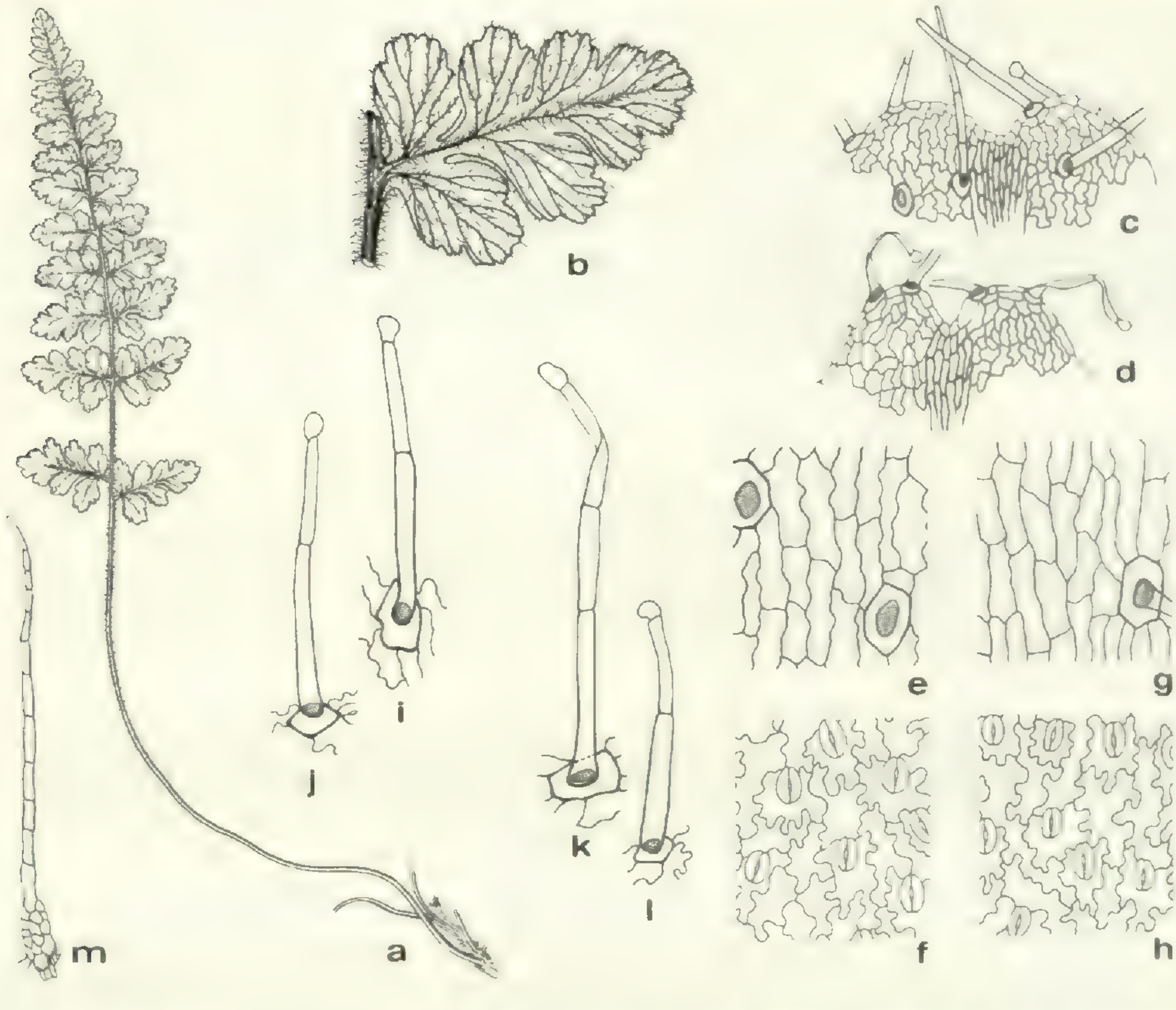


FIG. 20. *Eriosorus rufescens*: a, habit, × 1/3; b, pinna, × 1–1/3, both *Lehmann 4427* (US); c–d, margins with vein end and trichomes, × 20; c, *Mathews 1814* (G); d, *Lechler 2255* (GH); e–h, epidermis with basal cells of trichomes darker, all × 40; e, g, upper surface; f, h, lower surface; e, f, from large leaves, *Mathews 1814* (BM); g, h, *Lechler 2255* (GH); i–l, lamina trichomes, × 40; i, k, upper surface; j, l, lower surface; i, j, *Mathews 1814* (BM); k, l, *Lechler 2255* (GH); m, rhizome bristle, × 20, *Steyermark 57346* (US).

ized. The latter are restricted to páramos at higher altitudes, mainly in southern Colombia. The connections of *E. rufescens* with species at less specialized levels are not clear because there seems to be no convincing evidence to draw upon. A few collections from northern Peru [La Pucarilla, Cajamarca, *López & Sagástegui 5456, 6713, 6714* (GH)] have leaves which are less reduced and possibly relate to more generalized species. They seem best placed under *E. rufescens* on the basis of several details of the borders, veins and indument.

On deep mossy banks in ceja montaña, in shaded crevices of bluffs and on earth banks, at 2440–3600 m. Venezuela to Bolivia.

ADDITIONAL SPECIMENS EXAMINED: **Venezuela. Táchira:** Páramo de Tamá, *Steyermark 57346* (US). **Colombia. Cauca:** between Leja and Corrales, *Lehmann 4427* (B, K, P, US). **Ecuador.** *Pearce 250* (K). **Canar:** Cerro Yangu-

ang, e. of Azogues, *Fosberg & Prieto 22782* (US). **Peru. La Libertad:** Puerta del Monte, Pumatambo, *López & Sagástegui 3436* (GH). **Huánuco:** Carpish., *Ferreyra 10028* (USM); Pampayacu, *Kanehira 166* (GH, US); Muña, *Macbride 4302* (F, US), Playapampa, *4513* (F, US). **Cuzco:** Convención, Huadquiña, *Bües 972* (US), Valle San Miguel, *2142* (US); Prov. Urubamba, *Dreyfus*, Aug. 1941 (USM); Urubamba, Puyapata to Sayacmarca, *Vargas 2897* (US), Paucartambo, Tres Cruces, *12192* (GH). **Bolivia. La Paz:** Nor Yungas, Unduavi, *Buchtien*, Feb. 1914 (G, P), Dec. 24, 1908, *2165* (US), Nov. 1910, *2648* (S-PA, US); *Pearce*, Dec. 1865 (BM, K).

VARIANT INVOLVING ERIOSORUS RUFESCENS

The spores of the following collection are highly irregular and the rachises are strongly flexuose which suggests that it is an intermediate possibly with *E. flexuosus*. A collection of that species was made by Killip & Hazen from the forest, at a somewhat lower altitude, in the same locality. **Colombia. Tolima:** Quindío Trail, *Killip & Hazen 9494* (GH, NY, S, US).

11. **Eriosorus setulosus** (Hieron.) A. F. Tryon, comb. nov.

Fig. 21, Map 11

Gymnogramma setulosa Hieron. Engl. Bot. Jahrb. **34**:479. 1904. TYPE: *Lehmann 6180*, Colombia, in monte Páramo de Achupallas, inter Almaguer et La Cruz, 3000–3200 m. B! photo GH; isotypes: K! photo GH; P! photo GH; US!

Rhizome repent, the internodes short, ca. 3 mm. in diameter, with rigid, appressed trichomes or bristles, lustrous, deep brown, at the base 1 or 2 cells, the apical cell elongate or globose, glandular. *Leaves* erect, 13–42 cm. long. *Petiole* slender, terete near the rhizome, channeled near the lamina, castaneous, usually 2–4 times longer than the lamina, sparsely pubescent, denser near the lamina, the trichomes rigid, erect, ruddy brown, the apical cell elongate. *Lamina* linear, about the same width throughout or somewhat broader at the base, 1-pinnate, 3.5–17.0 cm. long, 1.5–3.5 cm. wide, determinate. *Rachis* straight, the upper surface sulcate, green near the apex, castaneous near the base, moderately to densely pubescent, the trichomes lustrous ruddy brown, bicolorous, usually lighter at the base, the apical cell elongate. *Pinnae* at right angles to the rachis or slightly ascending, usually elongate-ovate, the margins often crenate, incurved or plane with prominent basal auricles, more shallowly lobed above, 0.5–2.0 cm. long, 0.4–1.2 cm. wide, coriaceous; *upper surface* with sparse, rigid trichomes, bicolorous, ruddy brown, with a clear base, the apical cell elongate; *lower surface* with similar, denser trichomes; *stalk* 1–3 mm. on basal pinnae, often tan or green with decurrent lamina tissue; *veins* usually slightly raised from upper surface, terminating short of the margin, usually broadly clavate; *border* not differentiated or with 1 row of elongate cells, with many trichomes similar to those on the lamina surface. *Sporangia* most abundant on penultimate segments extending along main veins to the costa, the stalk of 2 tiers of unthickened cells, annulus of 16–21 cells. *Spores* tan or golden brown, the proximal face with tubercles and short ridges adjacent to the triradiate scar, with a broad, often irregular equatorial flange, the 3 angles projecting, the distal face with many prominent tubercles within the central areola.

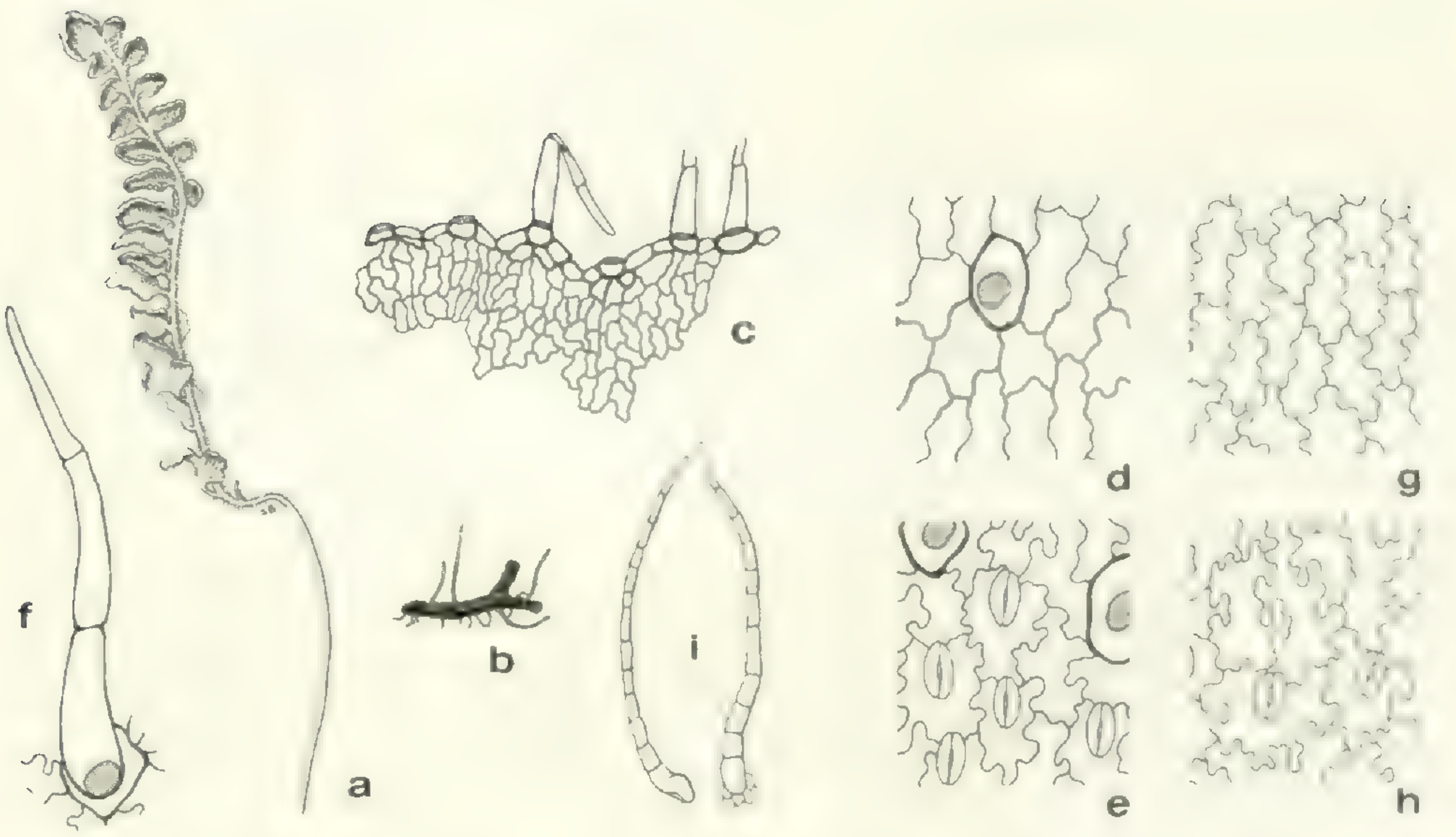


FIG. 21. *Eriosorus setulosus:* a, lamina with apical portion of the petiole, × 1/3, *Lehmann 6180* (US); b, rhizome from small plant with four petiole bases, the apex at left, × 1/3, *Tryon & Tryon 5958* (GH); c, margin with basal cells of trichomes, × 20; d, e, epidermis with basal cells of trichomes darker, × 40, d upper surface, e lower surface; f, trichome from lower surface of lamina, all × 40, *Lehmann 6180* (US); g, upper epidermis, h, lower epidermis, × 40; i, rhizome trichomes, × 10, all from *Tryon & Tryon 5958* (GH).

Eriosorus setulosus is a true páramo species occurring at the higher altitudes for the genus. It closely resembles *E. rufescens*, with which it occurs in southern Colombia. The larger guard cells shown in Fig. 21 e, h, suggest that it represents a high polyploid level. It occurs on the same páramo with *E. longipetiolatus* and with *Jamesonia Goudotii* in southern Colombia and has recently been collected with specimens of *Jamesonia Scammanae* by Sparre in northern Ecuador. Two other species, *Jamesonia verticalis* and *J. cinnamomea*, also occur on páramos in Cauca and represent a species group in that genus which is more closely allied to *E. setulosus* than to others in *Jamesonia*. The more reduced lamina cell size and spore irregularities in *E. setulosus* suggest that it may have a hybrid origin involving one of these species of *Jamesonia* and *E. rufescens*.

On páramos, in mossy banks, at 3000–3750 m., southern Colombia and Ecuador.

ADDITIONAL SPECIMENS EXAMINED: **Colombia. Cauca:** Páramo de las Papas, ca. laguna La Magdalena, *Idrobo* et al. *3089* (COL, GH); Páramo de Puracé, 25 km. e. of Popayan, *Tryon & Tryon 5958* (GH). **Ecuador. Carchi:** near Voladero, *Barclay & Juajibioy 9387* (GH); Páramo El Angel laguna oriente del Voladero, *Sparre 14199* (GH, S).

12. **Eriosorus longipetiolatus** (Hieron.) A. F. Tryon, comb. nov.

FIG. 22, MAP 11

Gymnogramma longipetiolata Hieron. Engl. Bot. Jahrb. 34:479. 1904. TYPE: *Lehmann 650*, Colombia, Nariño, páramos near Bordoncillo, 3300 m. B! photo GH; isotype: LE! photo GH.

Rhizome repent, the internodes long, ca. 2 mm. in diameter, with rigid, appressed trichomes or bristles, lustrous deep brown, at the base 1–3 cells, the apical cell globose, glandular. *Leaves* erect, 10–37 cm. long. *Petiole* slender, terete near the rhizome, subterete or shallowly channeled near the lamina, castaneous, shining, usually 3 or 4 times longer than the lamina, with sparse pubescence, the trichomes rigid, erect, ruddy brown, the apical cell elongate. *Lamina* linear, somewhat broader at the base, 1-pinnate, 4–8 cm. long, 1–2 cm. wide, determinate, the apical bud as large as adjacent segments. *Rachis* straight, the upper surface sulcate, green or tan especially near the apex, castaneous near the base, the trichomes lustrous ruddy brown, the apical cell elongate. *Pinnae* ascending (alternately disposed in two ranks), usually orbicular or cordate, the margins crenate, strongly incurved, 0.5–1.0 cm. long, 0.6–0.9 cm. wide, coriaceous; *upper surface* glabrous or with few rigid, lustrous deep brown trichomes, the apical cell elongate; *lower surface* more densely pubescent along the veins, the trichomes lustrous, deep brown with a clear base; *stalk* 0.5–2.0 mm. long, often tan or green with ridges continuous with those of the rachis; *veins* depressed in the upper surface, usually strongly clavate, short of the margin; *border* with a row of thick-walled cells about as long as broad, or irregularly dentate, with trichomes similar to the lamina surface. *Sporangia* most abundant on the penultimate veins extending along the main veins toward the rachis, the stalk of 3 unthickened tiers of cells (to one-half as long as the capsule), the annulus of 18–21 indurated cells. *Spores* tan or golden brown, the proximal face with broad ridges and papillae adjacent to the triradiate scar, with a broad, irregular equatorial flange, the angles strongly projecting, the distal face strongly papillate or tuberculate within and adjacent to the central areola, sometimes aborted.

The orbicular pinnae with strongly depressed veins are unique features of this páramo species. It appears most closely allied to, and has been collected with, *Eriosorus setulosus* on Páramo de las Papas in southern Colombia. *Jamesonia Goudotii* which also occurs there has pinnae disposed in two ranks and with strongly incurved margins. In the treatment of *Jamesonia* (1962) some collections from this páramo were included as variants of that species. Two other species, *Jamesonia verticalis* and *J. cinnamomea* also occur on the páramos of Cauca. The latter is especially similar to *E. longipetiolatus* in having orbicular pinnae.

On páramos in rock or wet places, at 3300 and 3530 m.

ADDITIONAL SPECIMENS EXAMINED: **Colombia. Cauca:** Páramo de las Papas, around Laguna La Magdalena, *Idrobo* et al. *3169* (COL, GH).

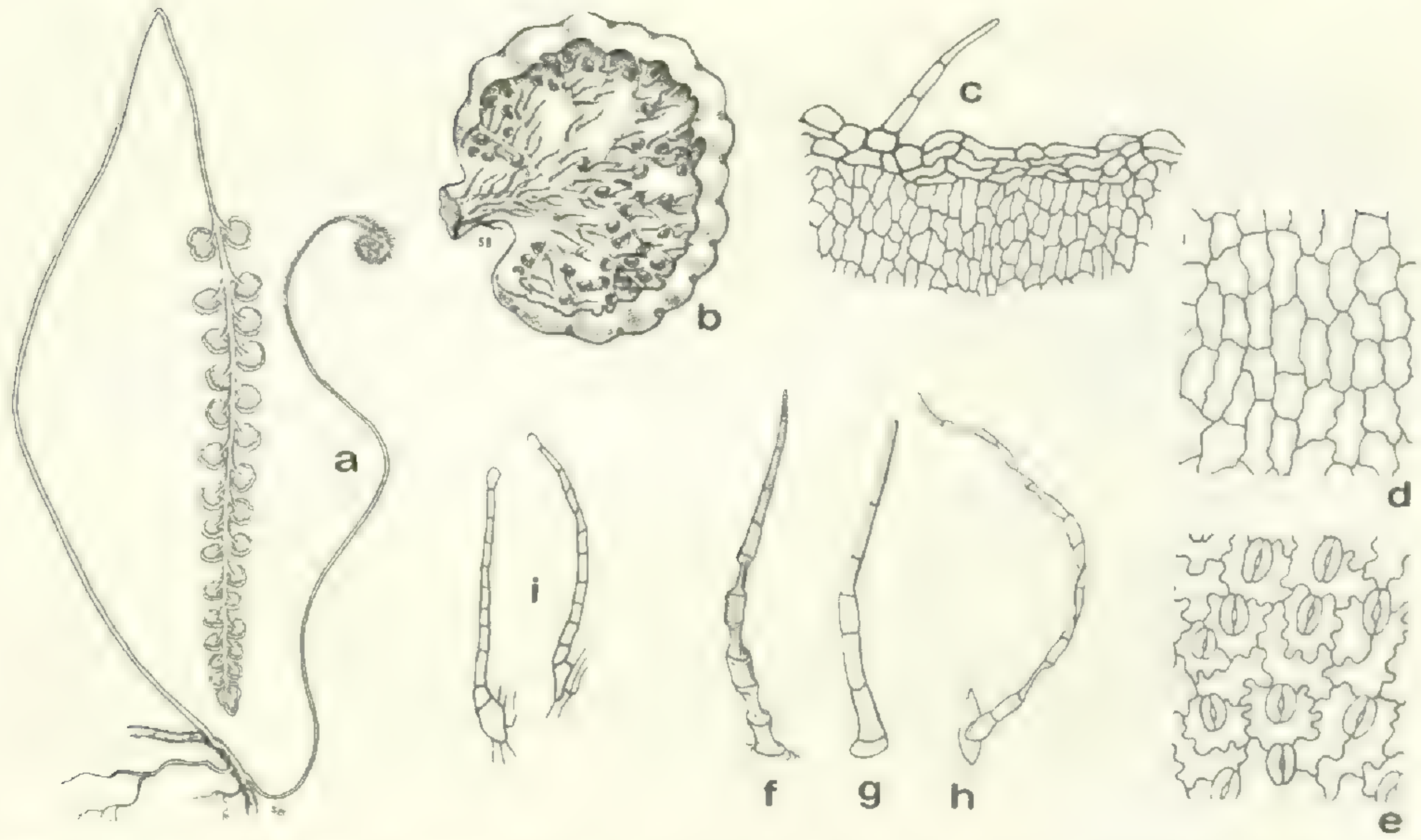


FIG. 22. *Eriosorus longipetiolatus:* a, habit, × 1/3; b, pinna, lower surface with sporangia, × 3–1/3; c, margin with trichome, × 20; d, upper epidermis; e, lower epidermis; f, g, lamina trichomes, f upper surface, g lower surface; h, petiole trichome, all × 40; i, rhizome trichomes, × 10, all from *Idrobo* et al. *3169* (COL).

13. **Eriosorus cheilanthoides** (Sw.) A. F. Tryon, Brit. Fern Gaz. 9:271. 1966

FIG. 23, 24, MAP 13

Grammitis cheilanthoides Sw. Syn. Fil. 23, 219, 419. 1806. TYPE: Tristan da Cunha (Mauritius in error). Herb. Swartz, S-PA! photo GH.

Asplenium filipendulaefolium Pet.-Th. Fl. Trist. d'Acugn. 34, t. 4, Oct. 1808. TYPE: *du Petit-Thouars*, Tristan d'Acunha, P! photo GH.

Gymnogramma filipendulaefolia (Pet.-Th.) Desv. Ges. Naturf. Berlin Mag. **5**:304. 1811.

Gymnogramma cheilanthoides (Sw.) Kaulf. Enum. Fil. 71. 1824.

Psilogramme cheilanthoides (Sw.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 335. 1882.

Gymnogramma elongata var. *brasiliensis* Brade, Arq. Jard. Bot. Rio de Janeiro **13**:64, t. 2, f. 3. 1954. TYPE: *Brade 15535*, Brazil, Pedra do Altar, perto da lagoa, Serro do Itatiaia, Rio de Janeiro, RB.

Rhizome repent, the internodes short, ca. 3–6 mm. in diameter, the trichomes or bristles rigid, appressed, ruddy to deep brown, at the base 1–6 cells wide, 1–3 cells thick, the apical cell elongate or globose. *Leaves* 8–90 cm. long. *Petiole* subterete at the rhizome, at the apex plane or channeled on the upper surface, from 1/12 to nearly equal the length of the lamina, with sparse pubescence, the trichomes crispate, clear or tan, the apical cell elongate. *Lamina* linear, the central pinnae slightly longer (up to four times longer than broad, in hybrid) the basal ones usually withered, 2-pinnate (1-pinnate in hybrids), 5.5–82.0 cm. long, 0.3–2.2 cm. wide, indeterminate, usually small, rarely larger than adjacent pinnae, pubescent. *Rachis* straight, plane or somewhat channeled on the upper surface, atropurpureous to castaneous, moderately to densely pubescent, the trichomes

clear or tan, the apical cell usually elongate, sometimes globose. *Pinnae* at right angles to the rachis, or somewhat ascending, elongate-ovate, equilateral, 0.5–1.2 cm. long, 0.2–0.7 cm. wide, herbaceous, subsessile; *upper surface* sparsely pubescent with crispate, clear or tan trichomes, the apical cell usually elongate, sometimes globose; *lower surface* with similar, usually longer, trichomes more tightly curled; *stalk* 0.5–2.0 mm., terete; *ultimate segments* cuneate, often bifurcate, the margins retuse, plane or somewhat inrolled; *veins* extending to or slightly short of the margin, the ends acute, not or slightly enlarged; *border* narrow, clear or opaque, 1–3 rows of elongate cells the apical portion protruding, rarely slightly irregular or with a few trichomes. *Sporangia* most abundant on the penultimate and base of ultimate veins, sometimes extending toward the pinna rachis, the stalk short, of 1 or 2 tiers on a cluster of clear cells, this often with a trichome, the annulus of 16–20 indurated cells. *Spores* usually deep brown sometimes slightly lighter, the proximal face with broad ridges or papillae adjacent to the triradiate scar, the equatorial flange narrow to moderately broad, the angles not projecting, the distal face with many small tubercles in the central areola, usually aborted in hybrids.

The high chromosome number and considerable morphological variation in *Eriosorus cheilanthoides* show that this species is more complex than can be shown in a formal taxonomic treatment. The available data suggest that hybridization may account for some of the diverse forms. Three hybrids are proposed after the main citations: the first two are readily distinguished by linear, 1-pinnate leaves and involve species of *Jamesonia;* the third has 2-pinnate leaves with long central pinnae, two to four times longer than broad, and appears to involve *E. flexuosus*. Some of the proposed hybrids occur in Ecuador, north of the range of the species; further data are needed to clarify their status.

The specimens from the South Atlantic islands of Tristan da Cunha have been critical in the interpretation of variation. The material that I have examined, from the first collection of Petit-Thouars in 1793 to the recent ones of Wace in 1956, provides samples of populations long isolated from related species. These show a considerable range of variation in size and leaf form. They were utilized for comparison with similar specimens of South America which often occur with other related species and with *Jamesonia*. There is a strong resemblance between specimens from Tristan, Brazil and some of those from Bolivia and Peru. This is shown by the linear, 2–pinnate, slightly pubescent leaves as well as details of the border cells, vein ends and rhizome indument.

Manton and Vida's report (1968) of a chromosome number of $n=174$ for *Eriosorus chelanthoides* from Tristan da Cunha

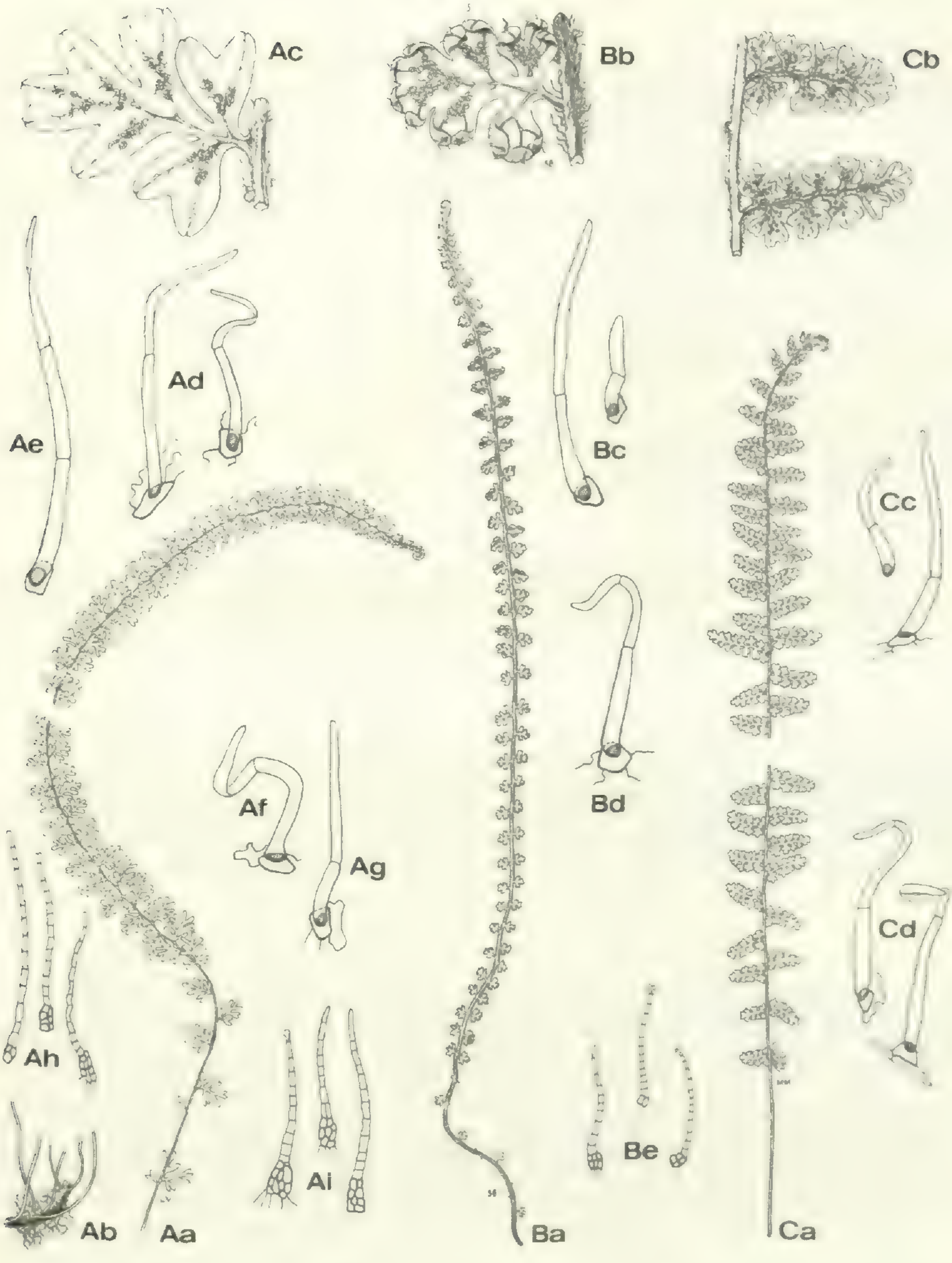


FIG. 23. *Eriosorus cheilanthoides* and hybrids: Aa–Ai *E. cheilanthoides:* Aa, portion of leaf, the central third omitted, with petiole apex, × 1/3; Ab, rhizome with petiole bases, × 1/3; Ac, pinna, × 1, all from *Tryon & Tryon 6724a,* Brazil (GH); Ad–Ag, lamina trichomes, × 40; Ad upper surface, Ae lower surface, *Plowman 2840,* Brazil (GH); Af upper surface, Ag lower surface, *Wace T36,* Tristan (A); Ah,Ai, rhizome bristles, × 10; Ah *Plowman 2840* (GH); Ai, *Wace T36* (A). Ba–Be *E. cheilanthoides* × *Jamesonia:* Ba, leaf with petiole apex, × 1/3, *Mathews 1091,* Peru (K); Bb, pinna, × 2–2/3, *Tryon & Tryon 5319,* Peru (GH); Bc,Bd, lamina trichomes, × 40; Bc upper surface, Bd lower surface, *Jameson,* Ecuador (NY); Be, rhizome bristles, *Tryon & Tryon 5319* (GH). Ca–Cd *E. cheilanthoides* × *E. flexuosus:* Ca, portion of leaf, the central third omitted, with petiole apex, × 1/3; Cb, pinna, × 1–1/3, *Steere,* Peru (US); Cc, Cd, lamina trichomes, × 40; Cc upper surface, Cd lower surface, *Jameson* (NY).

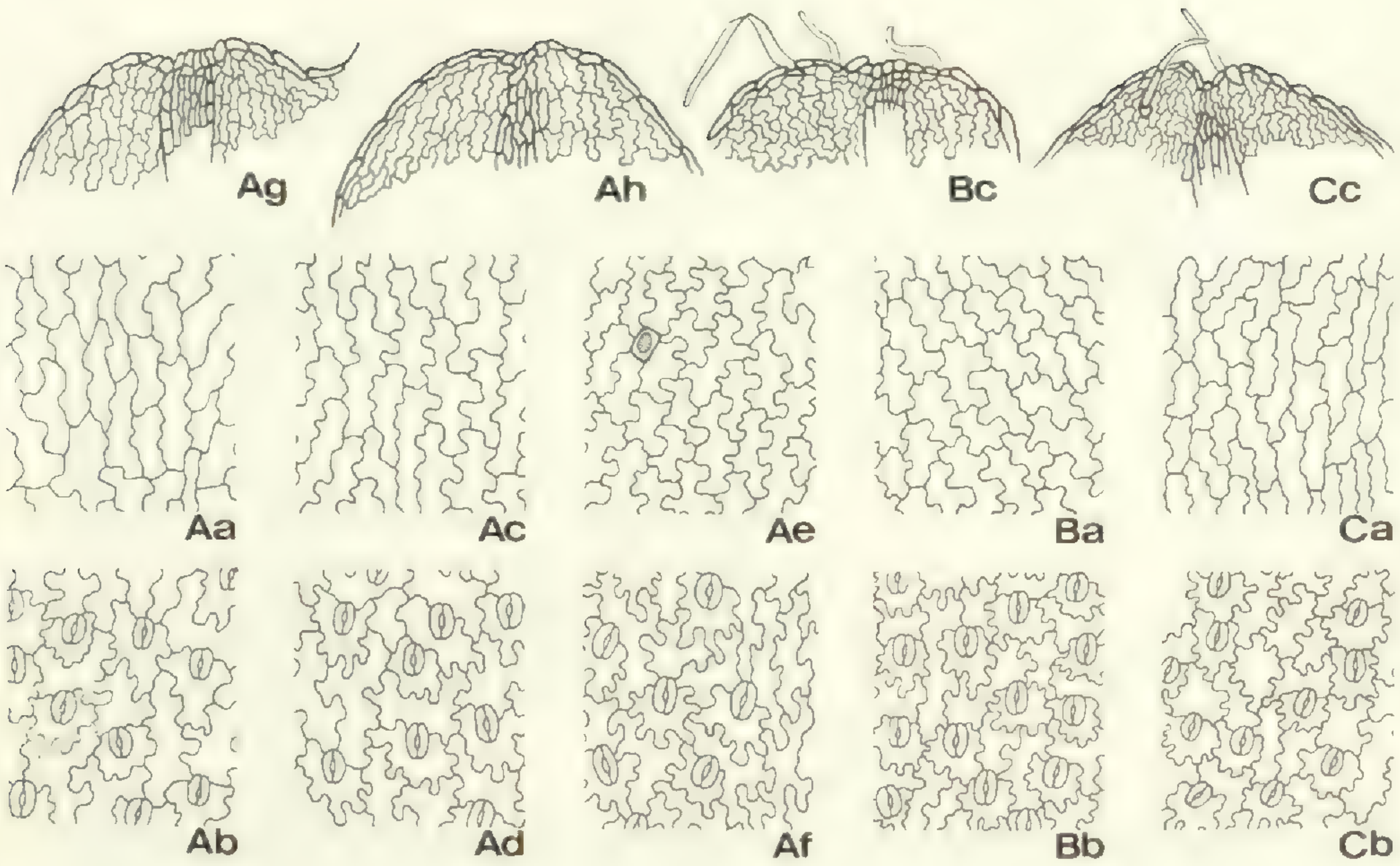


FIG. 24. *Eriosorus cheilanthoides* and hybrids: epidermal cells and margins on terminal portion of lobes. Aa–Ah *E. cheilanthoides:* Aa–Af, epidermis, the basal cell of trichomes darker, × 40; Aa, Ac, Ae, upper epidermis; Ab, Ad, Af, lower epidermis; Aa, Ab, *Wace T36,* Tristan (A); Ac, Ad, *Plowman 2840,* Brazil (GH); Ae, Af, *Buchtien 2736,* Bolivia (S); Ag, Ah, margins with vein end, × 20; Ag, *Wace T36* (GH); Ah, *Tryon & Tryon 6724a* Brazil (GH). Ba–Bc *E. cheilanthoides* × *Jamesonia:* Ba, upper epidermis; Bb, lower epidermis, × 40; Ac, margin with trichomes, × 20, *Jameson* Ecuador (NY). Ca–Cc *E. cheilanthoides* × *E. flexuosus:* Ca, upper epidermis; Cb, lower epidermis, × 40; Cc, margin with trichomes, × 20, *Jameson,* Ecuador (NY).

is interpreted by them as a dodecaploid based on 29. A count of $n=174$ is reported here for plants from Mt. Itatiaia. These high polyploids imply a complex history for the species. Lower chromosome-numbered elements are to be expected among the morphologically less specialized forms of the Andes. Specimens from Colombia, treated under *E. hirsutulus* may represent one of the lower chromosome levels but their affinity with other Colombian specimens and with *Jamesonia* suggest that they represent a parallel morphological development. Most collections treated as hybrids will key out to this species on the basis of the linear form of the lamina and the less elaborated pinnae. The collections from Brazil with 1-pinnate leaves are hybrids with *Jamesonia brasiliensis.* Andean collections with 1-pinnate leaves represent a complex of forms probably involving more than one species of *Jamesonia,* and their probable origin cannot be suggested on the basis of present information. Specimens with pinnae up to four times longer than broad represent another complex, probably related to *E.*

flexuosus. Hybrids between species of *Jamesonia* and *Eriosorus* seem to acquire the linear leaf form of *Jamesonia* which obscures the *Eriosorus* characters. Thus, there is some doubt as to whether *E. cheilanthoides* may be involved in all of the 1-pinnate specimens. It is not possible to identify such hybrids with confidence without information on the association of species or field observations. *Eriosorus cheilanthoides* is a complex entity at the 12-ploid level. It is possible that some of the lower chromosome levels may also be represented among the hybrids, especially those with well formed spores.

Peru and Bolivia, Mt. Itatiaia, Brazil and Tristan da Cunha Islands. In South America among rocks, at edge of boulders and open hillside at 2200–3600 m.; on the South Atlantic islands on peaty, rock ledges at 90–400 m.

ADDITIONAL SPECIMENS EXAMINED: **Peru. Ayacucho:** Pampalca, *Killip & Smith 23249* (F, GH, NY, S, US); above Yanamonte, *Weberbauer 5658* (B, F, GH, US). **Cuzco:** Huadquiña, *Bües 978* (US); Lucumayo valley, *Cook & Gilbert 1360* (US); entre Acanacu y Pillahuata, *Vargas* (Herb. Gunckel 7911), *16785* (GH), Cuzco, (Herb. Gunckel 7917) (GH), Paucartambo, 353, *3641, 12239,* Prov. Urubamba, Yanahuara, *9343* (GH). **Puno:** Agapata, *Lechler 2036* (B, F, G, K, P, W). **Bolivia. La Paz:** Yungas, *Bang 693* (E, GH, K, NY, US); Unduavi, Nordyungas, *Buchtien 889* (S-PA), *2736* (S-PA, US), *2738* (F, P), *2739* (S), *2741, 2743* (US); Hichuloma, *Cárdenas 866* (in part GH); Unduavi, *Rusby 329* (NY); between La Paz and Carioco, *Bro. Julio 223* (US); Prov. Larecaja, *Mandon 1549* (G, in part K, P); above Tolapampa, *R. S. Williams 1151* (GH, NY, US). **Cochabamba:** Langunillas, *Brooke 6196A* (F); Incachaca, *Steinbach 5194* (GH), Cuchicanchi, *9729* (F, GH, S-PA, in part F, US), Quebrada de Corani, *9857* (BM, F, GH, NY, S-PA, US). **Santa Cruz:** Comarapa, *Steinbach 8567* (F, GH, S-PA). **Brazil. Rio de Janeiro:** Mt. Itatiaia, planalto, near "Abrigo Reboucas" shelter house, *Plowman & Sucre 2840/5140* (GH); *Tryon & Tryon 6724a, 6724b* (GH). **Tristan da Cunha Islands. Tristan da Cunha:** *Carmichael* (B, BM, GH, K), *du Petit-Thouars* (BM, P); cliff above settlement, *Christophersen 202, 210* (O), above Sandy Point, *456* (C,O); *Hesse* (B); *Wace T36* (A, BM). **Inaccessible:** above Blenden Hall, *Christophersen 2378* (O), on the plateau, *2502* (O), plateau at west end, *2554* (O), *Stableford 129* (BM). **Gough Island:** near Upper Watersmeet, *Wace 75* (BM), Lower Watersmeet, *104,* Main Glen, above Upper Watersmeet, *137* (BM).

HYBRIDS INVOLVING ERIOSORUS CHEILANTHOIDES

1. Eriosorus cheilanthoides × Jamesonia brasiliensis

MAP 13

Gymnogramma longifolia Bak. Ann. Bot. **5**:484. 1891. TYPE: *Glaziou 7017,* Brazil, Prov. Río de Janeiro, K! isotypes: B! photos BM, GH; C!, NY!, P! photos GH, S.

MAP 13–15. MAP 13, *Eriosorus cheilanthoides*, dot; inset South Atlantic islands, Tristan da Cunha, 3200 km. southeast of Brazil, Gough, 352 km. southeast of Tristan; Hybrid, *E. cheilanthoides* × *Jamesonia brasiliensis*, rhomb.; hybrid, *E. cheilanthoides* × *Jamesonia*, star; hybrid, *E. cheilanthoides* × *E. flexuosus*, var. *flexuosus*, circle. MAP 14, *E. hirsutulus*, dot; variants 1, 2, 3 as cited in text. MAP 15, E. *Lindigii*, dot; variant, rhomb.

Gymnogramma elongata var. *itatiaiensis* Brade, Arq. Jard. Bot. Rio de Janeiro 13:64, t. 3, 5, f. 1, 2. 1954. TYPE: *Brade 15435*, Brazil, Rio de Janeiro, Pedra do Altar, 2450 m. Serra do Itatiaia, RB.

Gymnogramma jamesonioides Brade, op. cit. 64, t. 4, 5, f. 3. 1954. TYPE: *Brade 15536*, Brazil, Pedra do Eco, 2400 m. Serro do Itatiaia, RB; isotype: BM!

On the planalto of Mount Itatiaia I have studied plants of *E. cheilanthoides* and *Jamesonia brasiliensis* growing from the edges of the same boulder, the former mostly on the shaded sides or under overhanging rock and the *Jamesonia* in more sunny, exposed places. Where plants of these two

genera occur in close proximity there are aggregations of intermediates with aborted or irregular spores. Some of these forms have been recognized taxonomically and they do appear distinct when disassociated from the place of their collection. They are interpreted here as elements of a hybrid complex on the basis of field observations and iregularity of the spores. **Brazil. Rio de Janeiro:** Piedra do Altar, *Brade 15534* (F, G, NY, US); along road near shelter house "Abrigo Reboucas," *Tryon & Tryon 6698a, 6724c* (GH).

2. Eriosorus cheilanthoides × Jamesonia

FIG. 23B, 24B, MAP 13

Gymnogramma elongata Grev. & Hook. Hooker Jour. Bot. 1:61, t. 119. 1834. TYPE: *Jameson,* in 1832, Ecuador, Surucucho, near Cuenca, road to Naransal, mts. of "Peru," 9000 ft. Herb. Greville, E! photos BM, GH; isotype: Herb. Hook. K! photo GH.

Gymnogramma angustifrons Bak. Syn. Fil. 380. 1868, based on *Gymnogramma elongata* Grev. & Hook. not *Gymnogramma elongata* (Sw.) Hook. 1864, which is *Polypodium astrolepis;* an illegitimate name for the earlier homonym.

Psilogramme elongata (Grev. & Hook.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 335. 1882.

Eriosorus elongatus (Grev. & Hook.) Copel. Gen. Fil. 58. 1847.

The first hybrid involving *E. cheilanthoides* is proposed with some confidence as this occurs with only a single species of *Jamesonia* and both parental species have been studied at the same site. Most of the intermediates from the Andean area are more difficult to interpret and are treated as possible hybrids under the above general formula. Some have well formed spores but cannot otherwise be distinguished from other members of this hybrid complex. In a few cases it is possible to suggest the *Jamesonia* parent species, but without sufficient conviction to warrant formal recognition of the combination. For example, the specimens of *Pennell 13850,* from Cuzco, Peru have rigid pinnae appressed to the densely brown, tomentose rachis; the pinnae are glabrous to slightly pubescent beneath and the leaf has a large apical bud. In these characters, the collection resembles *Jamesonia Goudotii* and *J. Alstonii,* closely related species which both occur in Cuzco. The collection of *Wurdack 1161,* from Amazonas, Peru is from the same locality as his collection of *Jamesonia imbricata* var. *glutinosa* which was noted as being locally abundant in open, scrub forest. The former has dense, curled tomentum on the pinnae as in *Jamesonia.* The three collections from Bolivia probably have either *J. scalaris* or *J. brasiliensis* as one parent. The pinna margins are strongly inrolled and the pinna stalks are usually bent and overlaying the rachis, as in the latter species.

Ecuador to Bolivia. In cloud forest, in open, grassy páramo or shaded rock ledges, at 2500–3800 m.

ADDITIONAL SPECIMENS EXAMINED: **Ecuador.** *Jameson 1052* (B, P). **Bolívar:** Simiatug, Hacienda Talahua, *Penland 556* (US). **Canar:** Cañar y Biblián, *Barclay & Juajibioy 8721* (GH). **Azuay:** 37 km. w. of Cuenca, *Barclay & Juajibioy 8376* (GH); *Camp E-2012* (NY, US); above Sayaus, *Correll E354* (GH, S); Cuenca, *Pearce 189* (K); vic. of Toreador, *Steyermark* 53235 (US);

s. of Cuenca, *Wiggins 10819* (NY). **Loja:** Aug. 1847, *956* (K); *Seemann* (K); Hac. Horta-Naque, *Reinaldo Espinosa E193* (GH), *E881* (GH, US), Cerros de Acacana, *E1443* (GH); between San Lucas and Oña, *Hitchcock 21515* (US). **Santiago-Zamora:** region between Tambo Consuelo, *Camp E-1599* (F, NY). **Peru.** Andinamarca, *Mathews 1091* (K). **Piura:** Prov. Huancabamba, e. of Huancabamba, *Weberbauer 6096* (B, F, GH, US); road to Chanchaque, above Huancabamba, *Hutchison 1616* (GH), *Hutchison & Wright 6642* (GH). **Amazonas:** e. of Balsas, *Osgood & Anderson 84* (F, US); Cerros Calla Calla, above Leimabamba, *Hutchison & Wright 9678* (GH); Puma-urcu, se. of Chachapoyas, *Wurdack 1161* (GH). **Cajamarca:** Prov. Cutervo, *López & Sagástegui 5380* (GH); pass s. of Conchan, *Stork & Horton 10072* (US). **Libertad:** entre Unámen y Bolivar, *López & Sagástegui* 3332, Las Quinuas, *3348* (GH). **Junín:** Concepcion-Satipo, *Saunders 1078* (GH). **Huánuco:** Carpish Pass, *Ferreyra 8172, 10033* (GH); *Hodge 6272* (GH); Pampayacu, *Kanehira 143* (GH, US), *175* (US); *Stork & Horton 9910* (F, GH); *Tryon & Tryon 5319* (GH); Playapampa, *Macbride 4523* (F, US); Mito, *Macbride & Featherstone 1792* (F, G, US). **Cuzco:** Huadquiña, *Bües 981*, Valle Lares, *1777*, Vilcabamba, *2099*, La Convención, *2160* (US); Cerro de Cusilluyoc, *Pennell 13850* (F, GH, NY, S, US); Pillahuata, *Vargas 16784* (GH). **Bolivia. La Paz:** Cocopunco, *Tate 326* (NY, US); Pelichuco, *R. S. Williams 2604* (GH, NY, US). **Cochabamba:** Colomi, *Adolpho 106* (US); Pojos, *Steinbach 8367* bis (GH), Cuchicanchi, *6729* (in part F, US).

3. **Eriosorus cheilanthoides** × **Eriosorus flexuosus** var. **flexuosus**

FIG. 23C, 24C, MAP 13

Gymnogramma flabellata Grev. & Hook. Hooker Jour. Bot. 1:61, t. 120. 1834. TYPE: *Jameson*, in 1832, Ecuador, Surucucho, near Cuenca, road to Naransal, mts. of "Peru," 9000 ft. Herb. Greville, E! photo GH; isotypes: BM!, E! photos GH, K, NY; Herb. Hook. K!

Anogramma flabellata (Grev. & Hook.) Fée, Gen. Fil. 184. 1852.

Psilogramme flabellata (Grev. & Hook.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 336. 1882.

Eriosorus flabellatus (Grev. & Hook.) Copel. Gen. Fil. 58. 1947.

The collections with longer, more complex pinnae are difficult to assess for they are quite variable and are known only from fragmentary specimens. The collections of Jameson, Buchtien and Adolfo have somewhat flexuose rachises with tan and densely pubescent apices which suggest a possible relationship with *E. flexuosus*. One of the Buchtien collections and that of Cárdenas, noted below, are mixed with specimens of *E. cheilanthoides* which have well formed spores. The Ruiz, Pavon and Steere collections more closely resemble *E. chelanthoides* in their shorter pinnae with less bifurcate segments, straight rachises and dark brown, well formed spores. They may represent a variant form closer to *E. cheilanthoides* than the others included under the above hybrid name.

Ecuador, Peru and Bolivia. Among rocks in moist situations, at 3200–3600 m.

ADDITIONAL SPECIMENS EXAMINED: **Ecuador.** Prov. Cuenca, *Jameson 114* (K). **Peru.** Herb. Pavon 171 (G); Panatahuas, Prov. Tarma, *Ruiz 48* (B, US); Contumarca, *J. B. Steere* (GH, K, US). **Cuzco:** *Gunther 86* (S-PA). **Bolivia. La Paz:** Unduavi, Nordyungas, *Buchtien s.n.* (in part GH), *2735* (S-PA, US), *2742* (US); Hichuloma, *Cárdenas 866* (in part GH). **Cochabamba:** Colomi, *Adolfo 105* (US).

14. **Eriosorus hirsutulus** (Mett.) A. F. Tryon, comb. nov.

Fig. 25, Map 14

Gymnogramma hirsutula Mett. Ann. Sci. Nat., V, 2:209. 1864. LECTOTYPE: *Lindig 371*, Colombia, Cipacon, 2700 m., Herb. Mett. B! photo GH; isolectotypes: BM!, K!, P! photos GH, US.

Gymnogramma Karstenii Mett. op. cit. 210. 1864. TYPE: *Lindig 15d*, Colombia, Bogotá, B; isotypes: P! photos GH, US; NY! -frag.

Psilogramme hirsutula (Mett.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 340. 1882.

Psilogramme Karstenii (Mett.) Kuhn, op. cit. 340. 1882.

Rhizome repent, the internodes short, ca. 2–4 mm. in diameter, the trichomes or bristles rigid, appressed, ruddy to deep brown, at the base 1–3 cells, the apical cell elongate. *Leaves* erect or appressed and matted, 8–42 cm. long. *Petiole* subterete at the rhizome, at the apex plane or slightly channeled on the upper surface, from 1/8 to nearly equal the length of the lamina, sparsely pubescent, the trichomes rigid, erect, brown, or bicolorous with a lighter base, the apical cell elongate. *Lamina* lanceolate, the central pinnae slightly longer, the basal ones usually withered, 2-pinnate, 6–33 cm. long, 0.5–3.5 cm. wide, determinate, the apical bud small, usually minute, pubescent. *Rachis* strongly bent or sinuous, terete or slightly channeled on the upper surface, sparsely pubescent, the trichomes clear or bicolorous and darker in the upper portion, the apical cell elongate. *Pinnae* at right angles to the rachis or somewhat ascending, ovate or elongate-ovate, equilateral, 0.2–2.0 cm. long, 0.2–1.0 cm. wide, herbaceous, subsessile; *upper surface* sparsely pubescent, the trichomes clear or tan, usually curled, the apical cell elongate (rarely bulbous in variant); *lower surface* with similar somewhat denser trichomes; *stalk* 0.5–2.0 mm., slightly channeled or terete; *pinnules* cuneate usually bifid, scarcely imbricate, the margin sometimes retuse; *veins* ending short of the margin, usually well back of the border, the ends not or slightly enlarged; *border* narrow, of 1 or 2 rows of elongate cells, those at the apex shorter and irregularly projecting. *Sporangia* abundant on the penultimate and base of the ultimate veins, the stalk usually of 2 tiers or a cluster of clear or tan cells, often with a trichome, the annulus of 15–20 indurated cells. *Spores* tan, the proximal face with slender ridges or tubercles adjacent to the triradiate scar, the equatorial flange usually narrow, the angles slightly projecting, the distal face smooth, irregular or aborted in hybrids.

The collections of *Eriosorus hirsutulus*, mainly from the Department of Cundinamarca, Colombia, consist of specimens with well-formed, light brown or tan spores, and some, included as variants, with aborted or irregular spores. This species resembles *Eriosorus cheilanthoides* in having linear leaves. However, differences in the shape and disposition of the pinnae, vein ends, spores and the geographic ranges of the two suggest independent and perhaps a parallel evolutionary development of each. *Eriosorus hirsutulus* may represent one of the lower chromosome levels within the dodecaploid complex associated with *E. cheilanthoides*.

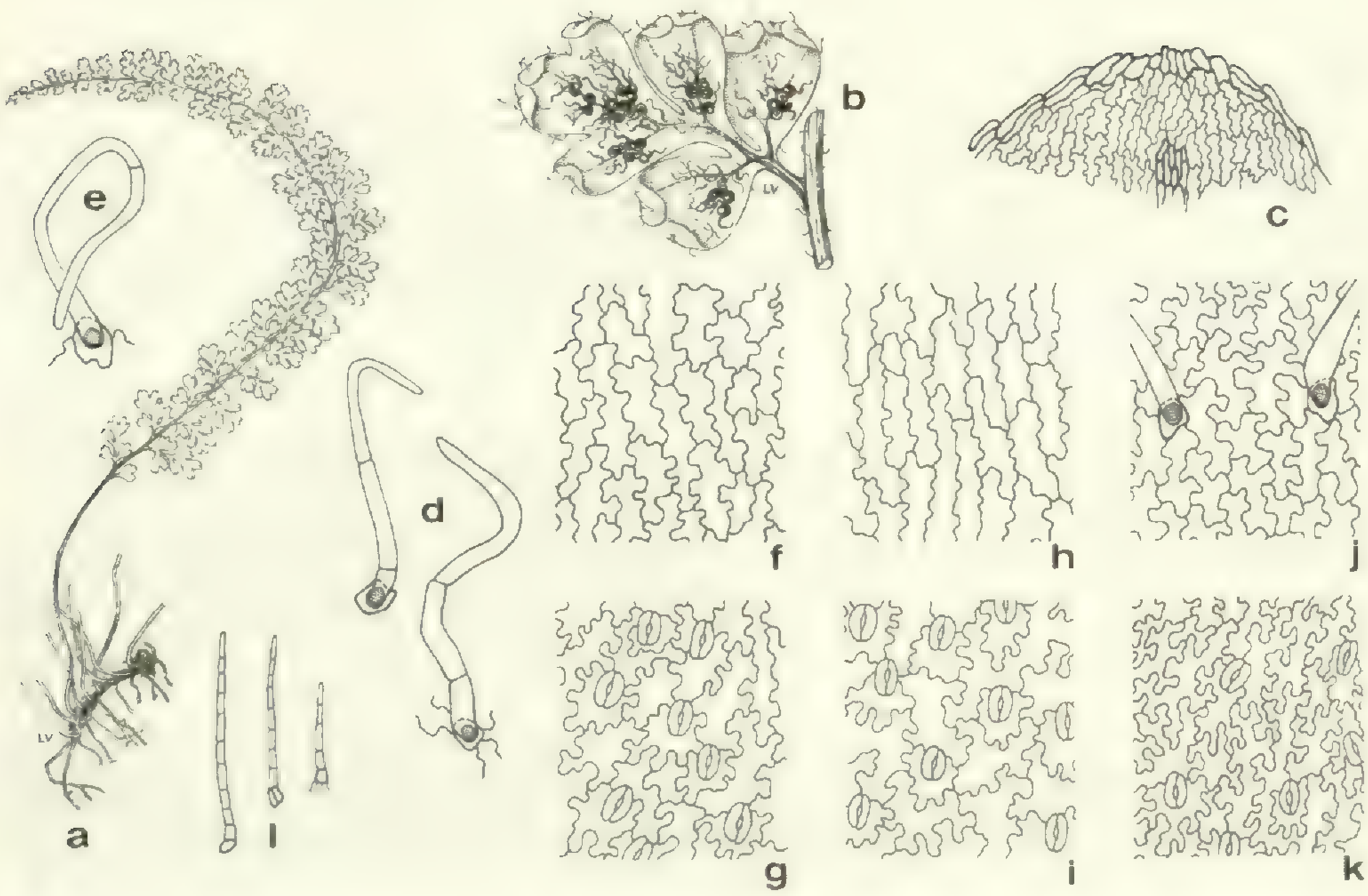


FIG. 25. *Eriosorus hirsutulus:* a, habit, × 1/3; b, pinna, × 2–2/3; c, margin with vein end, × 20, all from *Tryon & Tryon 6074* (GH); d, e, lamina trichomes, × 40, d upper surface, e lower surface, both *Lindig 371* (BM); f–k, epidermis, × 40; f, h, j upper surface, g, i, k lower surface, f, g *Lindig 371* (BM), h, i *Tryon & Tryon 6074* (GH); j, k *E. hirsutulus,* Variant 1, *Alston 7237* (GH); rhizome trichomes, × 10, *Lindig 371* (BM).

The variants, treated apart from the main citations, can be distinguished most readily by the presence of aborted spores. These plants may be of hybrid origin involving other species of *Eriosorus* or *Jamesonia* which are frequently found on the páramos of Colombia. On the basis of my own collections and field records, and from those of other collectors, it has been possible to reconstruct associations of some of the species from Cundinamarca. On Páramo Guasca, *E. hirsutulus* occurs at a somewhat lower elevation than *Jamesonia rotundifolia.* The variant with less dissected leaves resembling *Jamesonia* occurs with *E. hirsutulus* and *E. flexuosus* along road banks somewhat below the páramo. *Eriosorus flexuosus* has also been collected by Killip & Smith at the edge of Páramo de las Vegas and by the Littles near Monserrate.

The collection, *Lindig 371,* with well formed spores is taken as the type of *Eriosorus hirsutulus* instead of the other collection, *Lindig 15e,* cited by Mettenius, which I have not seen.

Colombia. Among rocks on peaty rock ledges and earth banks along road, at 3000–4200 m.

ADDITIONAL SPECIMENS EXAMINED: **Colombia. Boyacá:** Sierra Nevada del Cocuy, *Barclay & Juajibioy 7362* (GH). **Cundinamarca:** Los Gaques, *Alston 7491* (BM, GH), Boqueron de Chipaque, *7507* (BM, GH); Páramo de Coachi, *Bischler 2177* (COL); *Pennell 2238* (F, GH, NY, US); Bogotá, *Lindig 15c* (BM, K, P); Alto de Cruces Guadalupe, *Cuatrecasas 5561* (COL, F, GH, US); *Haught 5073* (S-PA); páramo e. of Guasca, *Little & Little 7443* (GH, US); *Tryon & Tryon 5922,* Páramo de Palacio, *6042,* 10 km. e. of Zipaquira, *6073, 6074* (GH). **Caldas:** Nevado del Ruiz, *Bischler 1459* (COL).

VARIANTS INVOLVING ERIOSORUS HIRSUTULUS WITH PUBESCENT LEAVES

1. On Páramo Guasca, northeast of Bogotá, *Jamesonia rotundifolia* occurs in abundance on the higher, wet sites, while plants of *Eriosorus hirsutulus* and this variant occur on road banks below the páramo. *Jamesonia* is probably genetically involved as shown by the cordate form, strongly inrolled pinnae and dense tomentum on the bud and rachis of the following collections. **Colombia. Norte de Santander:** La Mesita, Pamplona, *Alston 7237* (BM, GH); Ocaña, *Schlim 1017* (G). **Cundinamarca:** Bogotá, *Lindig 15* (BM), *15a* (B, BM, P); Guasca, *Tryon & Tryon 5922a* (GH).

2. The following collection has aborted spores and leaves with dense, rust colored tomentum on the rachis and pinnae of the same kind as in *Jamesonia bogotensis.* It has been collected with specimens of that species and there is also recorded, at a lower altitude, *Eriosorus flexuosus* from the edge of the páramo. **Colombia. Santander:** Páramo de las Vegas, *Killip & Smith 15652* (GH, NY, P, S).

VARIANT INVOLVING ERIOSORUS HISPIDULUS WITH GLANDULAR LEAVES

3. Specimens of the Little collection cited below are mixed with *Jamesonia imbricata* var. *glutinosa.* The glandular character of the variant implicates var. *glutinosa.* Specimens of *Eriosorus flexuosus* collected near Monserrate by the Littles, also show variation in the pinnae from compact-ovate to elongate-triangular, thus indicating a possible connection between that species and the variant under discussion. **Colombia. Cundinamarca:** Quebrada de Chico, *Cuatrecasas 5501* (COL, F, US); Bogotá, 3100 m., *Lindig 15b* in part, (B, K, P); Monserrate, *Little & Little 9447* (GH, US).

15. **Eriosorus Lindigii** (Mett.) Vareschi, Fl. Venez. 1(2):637. 1969

FIG. 26, MAP 15

Gymnogramma Lindigii Mett. Ann. Sci. Nat. V, 2:210. 1864. LECTOTYPE: *Lindig 15b,* Colombia, Bogotá, 3100 m. Herb. Mett. B! in part; isolectotypes: BM! K! P! photo GK. The collection consists of two elements and the name is applied to the specimens with smaller leaves, hispid glands and well formed spores. Portions of the collection *Lindig 15b* represent this species and are found in the following herbaria: B, left three leaves with rhizome and nearly complete leaves of packet material; BM, all three leaves; K, plant with rhizome and largest leaf; K, Herb. Hook. all five fragments; P, central plant with rhizome. The other specimens of this collection which have larger leaves, mostly eglandular trichomes, and aborted spores have been identified as variant a, under *Eriosorus hirsutulus.*

Psilogramme Lindigii (Mett.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 340. 1882.

Gymnogramma woodsioides Christ, Bull. Herb. Boiss. II, 7:274. 1907. TYPE: *Wercklé,* Colombia in 1906. Herb. Christ, P! photos GH, US; isotype: S-PA!

Rhizome repent, the internodes short, the trichomes crispate or rigid, appressed, golden to ruddy brown, at the base 1 or 2 cells, the apical cell globose, often with exudate. *Leaves* erect or lax and spreading, 8–36 cm. long. *Petiole* terete, lustrous-castaneous, 1/4 as long as to equal the length of the lamina, glabrous or sparsely pubescent, the trichomes crispate, tan or brown, the apical cell globose. *Lamina* linear, the same width throughout or with pinnae somewhat longer in the central portion, and withered at the base, usually 2-pinnate, 7–25 cm. long, 0.5–2.0 cm. wide, sometimes determinate, the apical bud usually minute. *Rachis* straight or rarely slightly fractiflex, terete or slightly channeled, castaneous, moderately to densely pubescent, the trichomes clear or light brown, the apical cell globose, usually covered with golden brown exudate. *Pinnae* usually slightly ascending, ovate or elongate-ovate, equilateral or nearly so, 0.3–1.7 cm. long, 0.2–0.8 cm. wide, herbaceous, subsessile; *upper surface* sparsely pubescent, the trichomes clear, the apical cell globose, glandular, with copious exudate, *lower surface* with similar glands somewhat denser along the veins; *stalk* 0.5–1.0 mm. terete; *pinnules* cuneate, rarely bifid, usually imbricate, the lobes acute with irregular margins, usually incurved; *veins* short of the margin, clavate or slightly enlarged; *border* narrow, 1 or 2 rows of mostly elongate cells, often projecting as papillae from the margin, those at the apex irregularly protruding adjacent to the vein, sometimes with a few glandular trichomes. *Sporangia* most abundant on the penultimate and basal portion of the ultimate veins, the stalk of 1 or 2 tiers subtended by a cluster of brown cells adjacent to the vein, the annulus of 12–20 indurated cells. *Spores* deep brown, the proximal face with few, slender ridges adjacent to the triradiate scar, with a narrow, often irregular equatorial flange, the angles not or slightly projecting, the distal face smooth or with few, low tubercles within the central areola, sometimes aborted or irregularly developed.

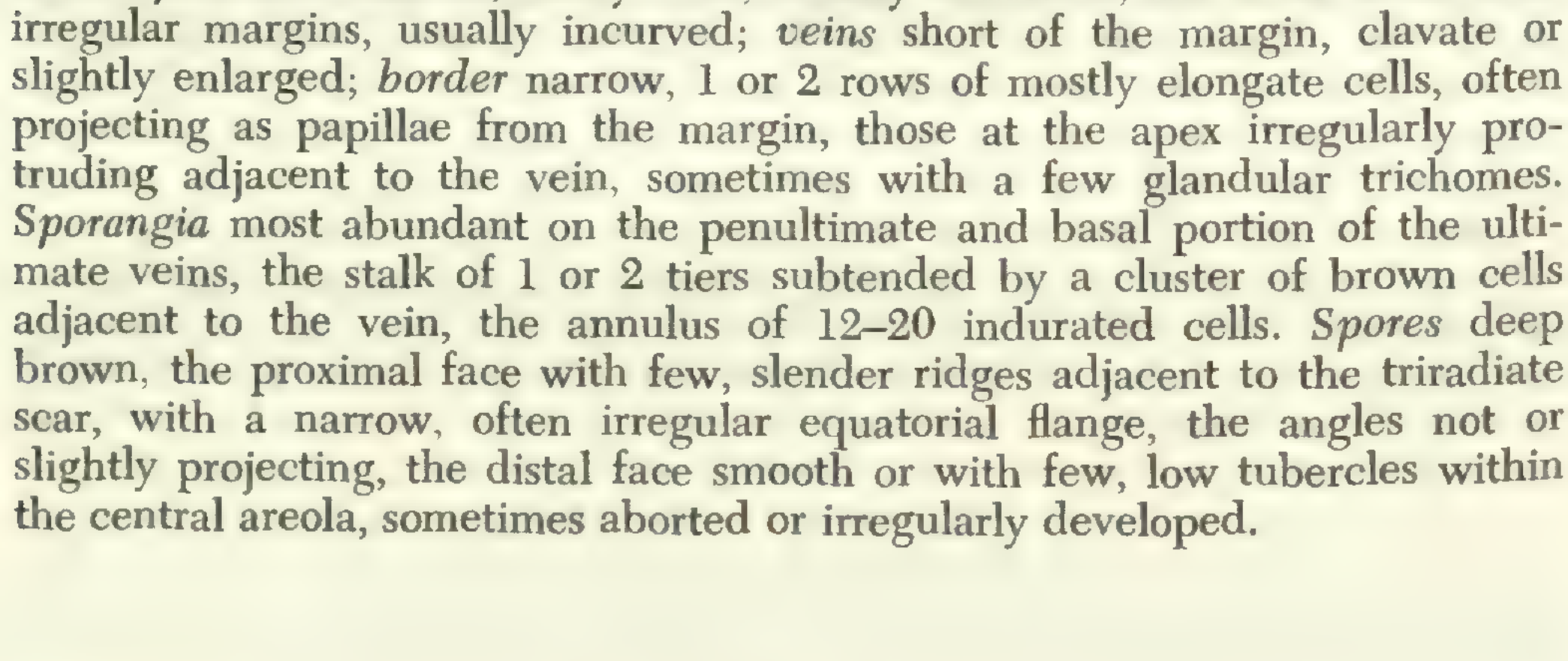


FIG. 26. *Eriosorus Lindigii:* a, habit, × 1/3, *Tryon & Tryon 6076* (GH); b, pinna, × 2–2/3; c, margin with short vein end, × 20; d, upper epidermis with glandular trichome; e, lower epidermis; f, g lamina trichomes, f upper surface, g lower surface, all × 40, *Lindig 15b* (P); h, rhizome trichomes, × 20, *Tryon & Tryon 6076* (GH).

Eriosorus Lindigii is most closely related to *E. hirsutulus* and possibly represents a stabilized intermediate of this and *Jamesonia imbricata* var. *glutinosa*. These three taxa occur on the páramos around Bogotá, but there is no record, at present, of their association together at any site. The variant, from La Calera, certainly represents an intermediate form involving *Jamesonia*. The patelliform shape and bent stalks of the pinnae, their dense glands and irregular margins are all characteristic of *Jamesonia*. The spores are entirely aborted in this collection. This taxon is recognized primarily on the basis of a unique association of characters found on the specimens cited. There is a preponderance of well formed spores. The plants occur on relatively distantly isolated páramos.

Cundinamarca, Colombia. On sandstone ledges or in shade at base of boulders, at 2800–3350 m.

ADDITIONAL SPECIMENS EXAMINED: **Colombia. Cundinamarca:** San Cristobal, *Bro. Apollinaire & Arthur 167* (US); Páramo Guasca, *Bro. Ariste-Joseph,* 1921 (C, K, NY, US); páramo above El Chico, *Fosberg 22031* (US); Páramo Cruze Verde, *Tryon & Tryon 6076* (COL, GH); Usaquén, *Uribe Uribe 215* (F).

The following collection of plants with mostly entire pinnae and aborted spores are intermediate to and probably involve hybridization with *Jamesonia imbricata* var. *glutinosa* which occurs on several of the páramos near Bogotá. **Colombia. Cundinamarca:** Páramo La Calera, 6 km. e. of Bogotá, *Tryon, Tryon & Idrobo 6150* (COL, GH).

16. **Eriosorus aureonitens** (Hook.) Copel. Gen. Fil. 58. 1947

FIG. 27, MAP 12

Gymnogramma aureonitens Hook. Icon. Pl. 9: t. 820. 1852 (prior to May, cf. Gard. Chron. 1852: 278). TYPE: *Lobb,* Peru, Veto K! photo GH; fragment NY! ex K.

Eriosorus scandens Fée, Gen. Fil. 152, t. 13B, f. 1. 1852 ("probably December," see W. T. Stearn, Webbia 17:207–222. 1962). TYPE: *Ruiz,* Peru; isotype Herb. *Pavon,* no. *153* G! photo GH.

Psilogramme aureonitens (Hook.) Kuhn Fests. 50 Jub. Reals. Berl. (Chaetop.) 341. 1882.

Rhizome repent, compact with short internodes, ca. 2–4 mm. in diameter, the trichomes or bristles rigid, ruddy to deep brown, at the base 1–4 cells wide, 1–3 cells thick, the apical cell globose. *Leaves* subscandent or scrambling, 50–62 cm. long (the longest incomplete). *Petiole* very slender, subterete at the rhizome, plane or slightly channeled on the upper surface and about 4 times as broad near the apex, atropurpureous, about 1/3 as long as the lamina, tomentose, the trichomes matted, ferrugineous, the apical cell elongate. *Lamina* elongate, the pinnae oriented in one plane with the central ones longer than those at the apex or base, 3-pinnate, 30–50 cm. long, 4–25 cm. wide, indeterminate, the apical bud large, densely tomentose. *Rachis*

fractiflex, subterete or slightly sulcate on the upper surface or plane, atro-purpureous, with dense, matted tomentum, the trichomes ferrugineous, crispate, the apical cell elongate. *Pinnae* strongly ascending, departing from the rachis at an acute angle, elongate-triangular, the basiscopic pinnules sometimes larger, 6–18 cm. long, 5–7 cm. wide, subcoriaceous; *upper surface* with matted ferrugineous tomentum, the trichomes often clear or lighter colored at the base, the apical cell elongate; *lower surface* with tomentum similar to the upper surface, usually denser along the veins; *stalk* 10–35 mm. long, terete with dense tomentum as on the rachis; *pinnules* deltoid, triangular or ovate; *ultimate segments* orbicular with margins crenate or dentate; *veins* protruding from the margin in a tooth, the vein ends enlarged, broadly clavate at the base of the tooth; *border* mostly one row, usually interrupted, the cells irregular, those at the vein end shorter, protruding and with numerous trichomes similar to those on the lamina surfaces. *Sporangia* dense along the veins to the costa, obscuring the pinnule surface, the stalk usually 1 tier of clear cells subtended by a cushion of clear or tan cells, the annulus of 15–22 indurated cells. *Spores* deep brown, the proximal face with broad ridges parallel to the triradiate scar and irregular tubercles in the angles of these and adjacent to the usually broad irregular equatorial flange, the angles projecting, the distal face with several large tubercles.

This is one of the unique species in that it possesses dense tomentum enveloping the large, scandent leaves. Similar indument occurs in several species, mainly of Venezuela, allied to and including *Jamesonia canescens*. However, the highly reduced linear leaves of these species of *Jamesonia* are wholly unlike those of *Eriosorus* and suggest that there has been a parallel development of the dense tomentum in the two genera. A dense, ruddy tomentum also occurs on the smaller, erect leaves of *E. Stuebelii* which also occurs in northern Peru. There are other resemblances to *E. Stuebelii* such as the disposition of the vein ends, the epidermal cells and spores. *Eriosorus aureonitens* is also similar to *E. accrescens* in the scandent habit of the leaves and long pinna stalks, and these two species occur in the same region in the Department of Amazonas, Peru. Both *E. Stuebelii* and *E. accrescens* are known only from Peru; they occur at higher altitudes up to 3300 m. and their spores are often irregularly formed. *Eriosorus aureonitens* has the widest range, growing from Colombia to southern Peru and occurring at lower altitudes. The spores are abundant, well formed and evidently are effective in species reproduction. The more limited record and abnormal spore development of the other species suggest that they are possibly intermediates involving hybridization with *E. aureonitens*.

Climbing or scrambling, locally frequent in open places, on moorland, between shrubs, and on clay banks in woods. Southern Colombia to southern Peru at 2750–3150 m.

FIG. 27. *Eriosorus aureonitens:* a, lamina and upper part of petiole, × 1/3; b, pinnule, upper surface with tomentum, × 2/3, both *Wurdack 1738* (GH); c, pinnule with tomentum removed, × 3–1/3, *Hutchison & Wright 5504* (GH); d, margin with protruding vein end and trichomes, × 20; e, upper epidermis, the basal cells of trichomes darker; f, lower epidermis, both × 40, all from *Wurdack 1738* (GH); g, rhizome trichomes, × 10, *Hutchison & Wright 5504* (GH).

ADDITIONAL SPECIMENS EXAMINED: **Colombia. Tolima:** Alto de Oseras, *Lehmann 2398* (B, BM, G). **Ecuador. Loja:** between Saraguro and San Lucas, *Lehmann,* on Aug. 30, 1878 (GH-frag. ex W). **Peru.** Pacasmayo to Moyobamba, *Stübel 1024* (B). **Amazonas:** Leimebamba to Balsas road, *Hutchison & Wright 5504* (UC, GH); *Wurdack 1738* (GH, US). **Junín:** Vitoc, *Lobb,* 1854 (BM). **Huánuco:** Huánuco to Pampayacu, *Kaneira 153* (GH, US); Playapampa, *Macbride 4529* (F, US). **Puno:** Sandia to Chunchusmayo, *Weberbauer 1310* (B).

17. **Eriosorus accrescens** A. F. Tryon, Rhodora **65**:57. 1963

FIG. 28, MAP 12

TYPE: *Vargas 2921,* Peru, Prov. Urubamba, Puyupata, US!

Rhizome not seen. *Leaves* subscandent or leaning, not erect (all specimens incomplete), 21–45 cm. long. *Petiole* very slender, subterete at the rhizome, plane or slightly channeled on the upper surface and about 4 times as broad near the apex, atropurpureous, ca. about 1/3 as long as the lamina, densely pubescent, the trichomes somewhat matted, tan, the apical cell with an elongate apex. *Lamina* elongate-trullate with the pinnae oriented in one plane, the central ones longer; the basal pinnae are often withered, 3-pinnate, 15–56 cm. long, 6–16 cm. wide, indeterminate, the apical bud large and densely tomentose. *Rachis* straight or usually somewhat flexuose, plane or slightly sulcate on the upper surface, castaneous, becoming lighter colored toward the apex, tomentose, the trichomes tan, crispate, the apical cell elongate. *Pinnae* ascending, departing from the rachis at an acute angle, elongate-triangular or deltoid, the basiscopic pinnules often larger, 4–12 cm. long, 3–6 cm. wide, subcoriaceous; *upper surface* with sparse to moderately dense pubescence, the trichomes clear or tan, the apical cell elongate; *lower surface* with matted, fulvous indument, denser along the veins, the trichomes similar to those of the upper surface; *pinnules* ovate or elongate-triangular to deltoid; *ultimate segments* ovate or orbicular with crenate margins; *veins* terminating at the margin in a shallow sinus, not or rarely protruding, usually broadly clavate; *border* narrow, with 1–3 rows, irregular, usually with one discontinuous row of cells, those adjacent to the vein end shorter, protruding, with many trichomes similar to those of the lamina surface. *Sporangia* dense along the veins to the costa, sometimes obscuring the surface of the segment, the stalk of 1 or 2 tiers subtended by a cushion of clear or tan cells, the annulus of 17–20 indurated cells. *Spores* deep brown, the proximal face with irregular tubercles often coalescent in a ridge adjacent to the triradiate scar, the equatorial flange usually broad, often irregular, the angles not or slightly projecting, the distal face with several large tubercles.

All of the specimens are incomplete but the long petioles, broadest at the apex, and the long pinna stalks are suggestive of a scandent leaf habit. In these characters, as well as the general form of the leaves and indument, the species resembles *Eriosorus aureonitens*. The leaves of *E. accrescens* are not densely tomentose as in the former, and differ in having broader, more strongly lobed ultimate segments and veins ending in a sinus at the margin.

Both species occur in dense shrubby vegetation dominated by bamboo, in the Departments of Amazonas and Puno, Peru.

In wooded ravine in shrubby vegetation with bamboo, in shade, Peru, at 2800–3350 m.

ADDITIONAL SPECIMENS EXAMINED: **Peru. Amazonas:** entre Leimebamba y Balsas, *López* et al. *4444* (GH). **Cuzco:** Huadquiña, *Bües 992* (US), Valle de Lares, Montaña de Cola, *1925* (US), Altura de Chaco *2135* (US). **Puno:** Sandia, *Weberbauer 733* (B, USM).

18. **Eriosorus Stuebelii** (Hieron.) A. F. Tryon, Rhodora **65**:57. 1963

FIG. 29, MAP 12

Gymnogramma Stuebelii Hieron. Hedwigia **48**:219, t. 9, f. 5. 1909. TYPE: *Stübel 1058*, Peru, Mojon-Cruz, inter Pacasmayo et Moyobamba B! photo and fragment GH!

Rhizome repent, the internodes short, compact, ca. 2–3 mm. long, the trichomes or bristles crispate or rigid and appressed, atropurpureous to deep brown, at the base 1–4 cells wide, 3 cells thick, the apical cell globose. *Leaves* erect, 24–28 cm. long. *Petiole* slender, terete, at the apex 2 or 3 times broader than the base, plane or slightly sulcate on the supper surface, about 1/3 as long as the lamina, tomentose, the trichomes matted, ferrugineous, the apical cell elongate. *Lamina* elongate-triangular, the basal pinnae sometimes smaller than the central ones, 2-pinnate, 8–22 cm. long, 2–8 cm. wide, determinate, the apical bud large, densely tomentose. *Rachis* straight, subterete or slightly sulcate on the upper surface, atropurpureous with dense, matted tomentum, the trichomes ferrugineous, crispate, the apical cell elongate. *Pinnae* slightly ascending or at right angles to the rachis elongate-triangular or -ovate, the basiscopic pinnules slightly larger, 2.5–4.5 cm. long, 1.5–2.0 cm. wide, subcoriaceous; *upper surface* with matted ferrugineous or fulvous tomentum, the trichomes clear, or tan, the apical cell elongate; *lower surface* sparsely to moderately pubescent, somewhat denser on the pinna rachis, the trichomes similar to those of the upper surface; *stalk* subsessile, the basal pinnae with stalks 1–3 mm. long, slightly channeled on the upper surface, tomentose; *pinnules* ovate, often with few shallow lobes, the margins crenate; *veins* terminating at the margin or slightly projecting in a tooth, broadly clavate; *border* of 1 row of elongated cells, those at the pinnule apex shorter, irregularly protruding with trichomes similar to those of the lamina surface. *Sporangia* abundant, dense along the veins to the costa, obscuring the abaxial surface, the stalk of one tier of elongated cells subtended by a cushion of shorter cells, the annulus of 16–23 indurated cells. *Spores* deep brown, the proximal face with broad ridges parallel to the triradiate scars, the equatorial flange usually broad, somewhat irregular, the angles projecting, with many coarse tubercles on both faces, sometimes very irregular or shriveled.

This species is known from the original collection made in northern Peru about a hundred years ago, and from a recent one made by César Vargas in southern Peru. The new material is

FIG. 28. *Eriosorus accrescens:* a, upper portion of lamina, × 1/3, *Vargas* 2921 (US); b, pinna, with lower pinnule cleared of indument, × 2/3, *Bües 2135* (US); c,d, pinnules, upper surface with pubescence, × 2/3; c, *Lopez* et al. *4444* (GH); d, *Vargas 2921* (US); e, margin with vein end, × 20; f, g, epidermis × 40, f upper epidermis, g lower epidermis, both *Vargas 2921* (US).

placed with the earlier collection, mainly on the basis of the similarity of the leaves which have subsessile pinnules and dense indument. It differs somewhat in having veins slightly protruding, as shown in Fig. 29d, and in this respect resembles *Eriosorus aureonitens*. The larger leaves and long pinnae stalks in that species are perhaps related to their scandent or scrambling habit. The plants occur in dense vegetation at low altitudes. The compact leaf form in *E. Stuebelii* is probably better adapted to the more open habitats at higher altitudes. The shriveled spores and variability in shape and orientation of the guard cells (Fig. 29, g, i) in these specimens are noteworthy.

In woods, Peru, at 3300 m.

ADDITIONAL SPECIMEN EXAMINED: **Peru. Puno:** bajando a Cachi-Cachi, Prov. Sandia, August 6, 1967, *Vargas 11834* (GH).

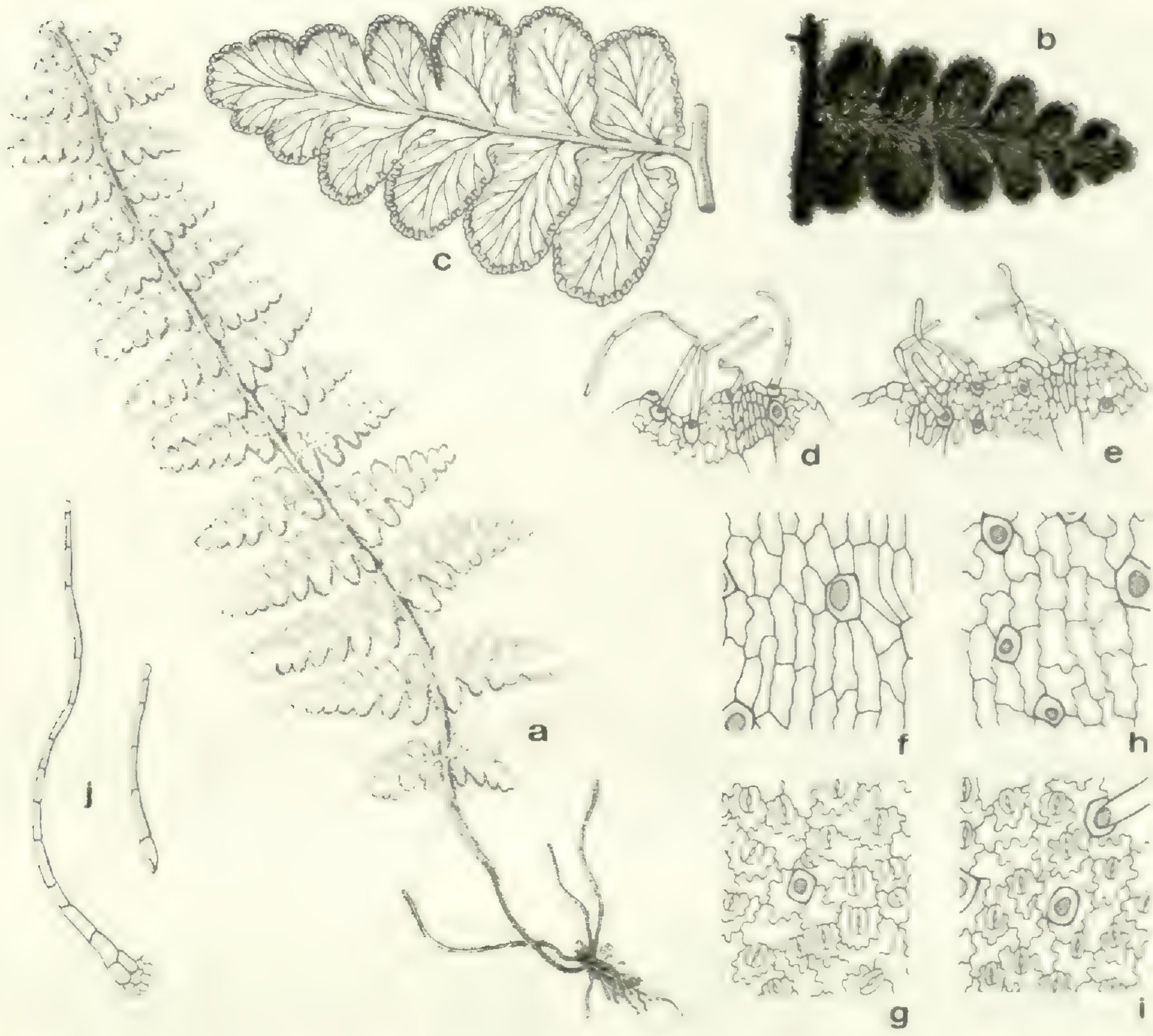


FIG. 29. *Eriosorus Stuebelii:* a, habit, × 1/3; b, pinna, upper surface with tomentum, × 1; c, pinna, lower surface with veins, the tomentum removed, × 1; d, e, margins with vein ends and trichomes, × 20, all from *Vargas 11834* (GH); e, *Stübel 1058* (GH); f–i, epidermis, with basal cells of trichomes darker, × 40; f, h upper surface, g, i lower surface; f, g *Stübel 1058* (GH); h, i *Vargas 11834* (GH); j, rhizome trichomes, × 10, *Vargas 11834* (GH).

19. **Eriosorus Wurdackii** A. F. Tryon, spec. nov.

FIG. 30, MAP 16

Rhizoma internodiis brevibus trichomatibus atrofuscis vel nigris ad basim cellulis 1–4 plerumque 2 latis, lamina elongato-triangularis plerumque 2- vel 3-pinnata apice determinato gemma glabra, rhachis plus minusve fractiflexa castanea vel atropurpurea in axillis pinnarum trichomatibus atropurpureis brevibus rigidis, pinnae elongato-triangulares rigido-herbaceae, pinnulae ovatae vel deltoideae adaxialiter glabrae abaxialiter sparsim pubescentes, nervi ad marginem vel paene attingentes extremis plus minusve clavatis, sporangia plerumque in fascia submarginali, sporae atrofuscae.

TYPE: Peru. Dept. Amazonas, Prov. Chachapoyas, 6–8 km. west of Molinopampa, in rock crevices in Jalca zone, 2200-2300 m., July 31, 1952, *J. J. Wurdack 1514* GH; isotype US.

Rhizome elongate, repent, the internodes short, ca. 4–7 mm. in diameter, the trichomes or bristles rigid, appressed, deep brown to nearly black, at the base 1–4, often 2, cells wide, 1 or 2 cells thick, the apical cell elongate. *Leaves* erect, 26–46 cm. long. *Petiole* subterete near the rhizome, at the

apex channeled, atropurpureous, equal to or slightly longer than the lamina, glabrous or with sparse, rigid, erect, brown trichomes, the apical cell elongate. *Lamina* elongate-triangular, the base broader than the central portion, 3- or mostly 2-pinnate, 16–22 cm. long, 3–13 cm. wide, determinate, the apical bud glabrous. *Rachis* somewhat fractiflex, the upper surface strongly channeled, castaneous or atropurpureous, sparsely pubescent, with tufts of trichomes at the pinnae axils, the trichomes tan to deep brown, or the base clear, the apical cell elongate or globose. *Pinnae* descending slightly from the rachis at an angle greater than 90 degrees, with the apex ascending, elongate-triangular, the basiscopic side sometimes slightly larger, 0.2–7.5 cm. long, 2–3 cm. wide, rigid herbaceous; *upper surface* glabrous; *lower surface* sparsely pubescent, the trichomes on veins among sporangia, clear, brown or bicolorous, the apical cell acuminate; *stalk* 0.3–1.0 mm. long, sulcate, the ridges of the upper surface continuous with those of the rachis; *pinnules* ovate or deltoid and shallowly lobed; *ultimate segments* orbicular or ovate, the margins crenate, plane; *veins* extending to or slightly short of the margin, terminating adjacent to a shallow sinus, somewhat enlarged to clavate; *border* narrow, clear with 1–3 rows of elongated cells, the cells at the vein end irregular, about as long as broad. *Sporangia* mostly on ultimate and penultimate veins, usually localized in a discrete submarginal band, the stalk of 1 or 2 tiers of cells subtended by a cushion of clear cells, the annulus of 18–23 indurated cells. *Spores* deep brown, the proximal face with prominent ridges parallel to the triradiate scar, the equatorial flange narrow, the 3 angles not projecting, the distal face smooth within the central areola.

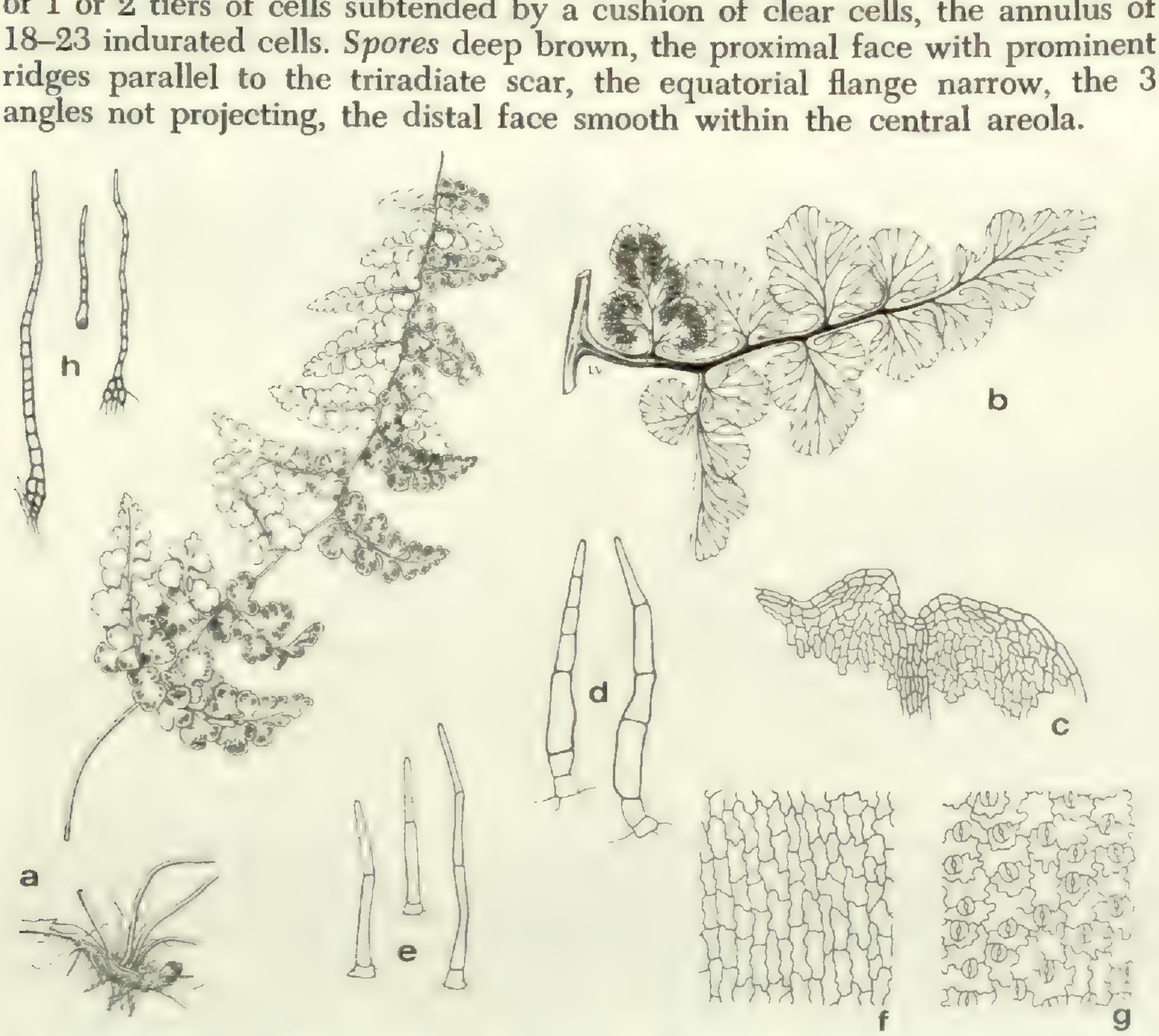


FIG. 30. *Eriosorus Wurdackii:* a, habit with about two-thirds of the petiole omitted, × 1/3; b, pinna with sporangia and trichomes on acroscopic pinnule, × 1; c, margin with vein end, × 20; d, trichomes from pinna axil; e, lamina trichomes from sorus; f upper epidermis, g lower epidermis, all × 40; h, rhizome bristles, × 10, all from *Wurdack 1541* (GH).

The species, known from this single collection from northern Peru, supplies a possible link with the distinctive scandent species, *Eriosorus Orbignyanus*. This relationship is shown by the peculiar habit of the pinnae descending from the rachis at an angle greater than 90 degrees, the sori usually forming submarginal bands and the veins often terminating short of the margin. *Eriosorus Wurdackii* is regarded as less specialized than *E. Orbignyanus* on the basis of its erect habit and simpler leaf form.

The submarginal sorus bands are unusual in *Eriosorus*. This, in addition to several other aspects of the plants, such as the firm texture of the pinnae, dark brown trichomes confined largely to the sorus among the sporangia, and the vein ends terminating short of the margin, suggests a connection with the genus *Pterozonium*. Two of the most widely distributed members of that genus, *P. reniformis* and *P. brevifrons* occur in northern Peru. A collection of the latter was also made by Wurdack in the same area as this new species of *Eriosorus*. *Pterozonium* represents a more specialized genus with once pinnate or simple leaves. It is certainly more closely related to *Eriosorus* than to other genera, and *E. Wurdackii* provides a possible link between them.

I am pleased to name the species for Dr. John Wurdack, whose fine collections of *Eriosorus* and the related genera, *Jamesonia* and *Pterozonium* from Peru, and the Guayana and Venezuelan highlands, supply some of the basic data for our knowledge of these genera.

20. **Eriosorus Orbignyanus** (Kuhn) A. F. Tryon, Rhodora **65**:56. 1963

Fig. 31, Map 16

Gymnogramma Orbignyana Kuhn, Linnaea **36**:70. 1869. TYPE: *D'Orbigny* 299, Bolivia, Cochabamba, Yuracarés, Herb. Mett. B! photo GH; isotypes B! G! photo GH; P! paratype: *D'Orbigny 174*, Bolivia. La Paz, Yungas, Herb. Mett. B! photo GH; isoparatypes: G!, P! photos GH.

Gymnogramma prehensibilis Bak. Syn. Fil. ed. 2. 517. 1874. TYPE: *Pearce*, July, 1866, Bolivia. La Paz, Sandillani, 8000–9000 ft. K! photo GH.

Psilogramme Orbignyana (Kuhn) Kuhn, Fests. 50 Jub. Real. Berl. (Chaetop.) 338. 1882.

Rhizome not seen. *Leaves* scandent or scrambling, 3 m. long. *Lamina* elongate, pinnae oriented in one plane, the central ones longer than the apical, 4-pinnate (largest incomplete specimen, ca. 95 cm. long, 18 cm. wide), indeterminate, the apical bud minute, slightly pubescent. *Rachis* fractiflex, the upper surface strongly channeled, the lower surface convex, castaneous, somewhat lighter near the apex, sparsely pubescent or glabrous,

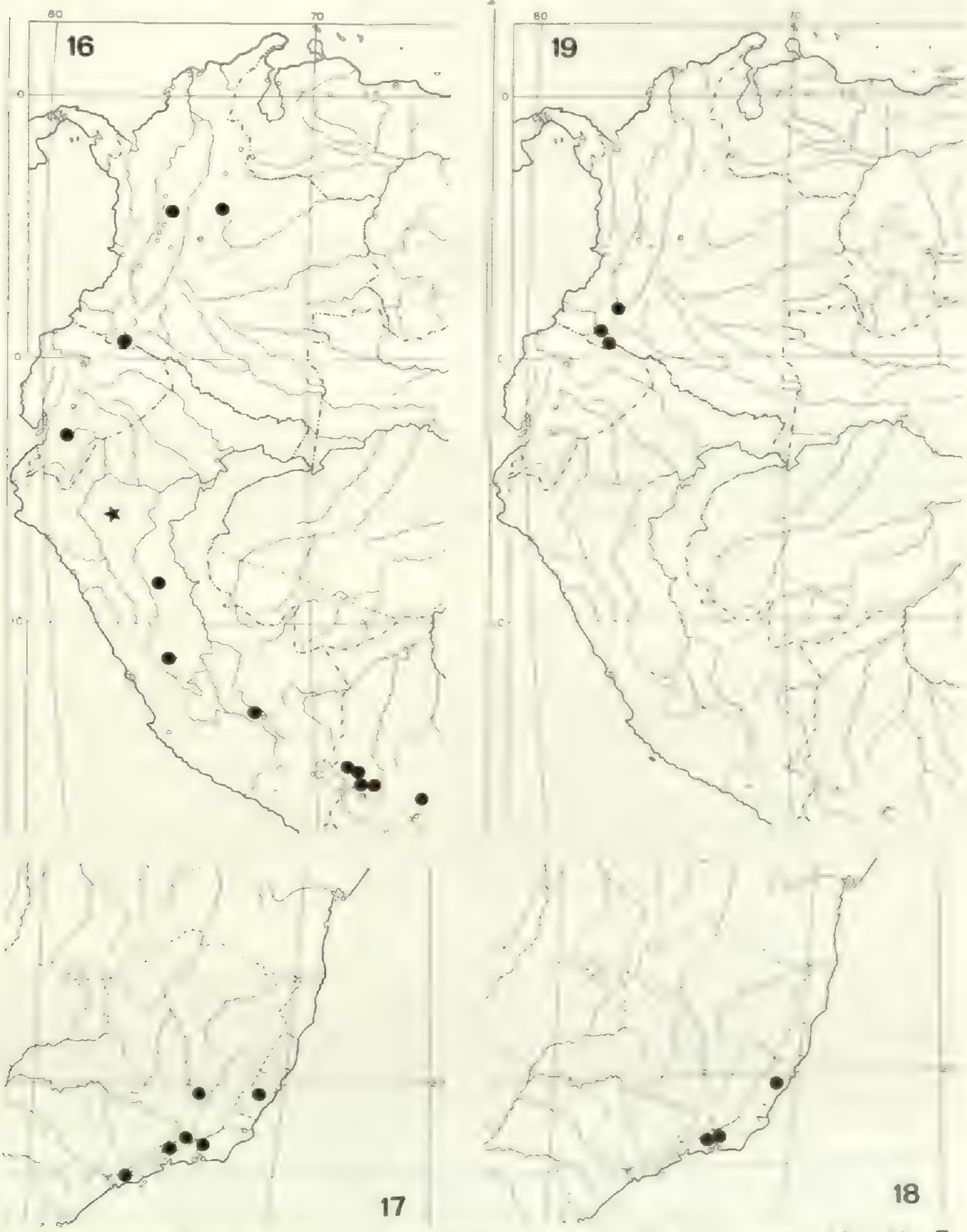
with tufts of trichomes in the pinnae axils, the trichomes tan or brown, with the apical cell elongate. *Pinnae* descending from the rachis, departing at a wide angle, greater than 90° (the pinna rachises fractiflex, the pinnule stalks strongly curved, forming arcs ascending toward the pinna apex) elongate-triangular or ovate, the basiscopic side sometimes slightly larger, 10–45 cm. long, 9–18 cm. wide, herbaceous or papyraceous; *upper surface* slightly pubescent, the trichomes clear, the apical cell elongate; *lower surface* pubescent, the trichomes similar, denser than the upper surface especially among the sporangia; *stalk* 10–40 mm. long, sulcate, ridges of the upper surface continuous with those of the rachis, slightly pubescent; *pinnules* elongate-triangular or ovate; *ultimate segments* usually orbicular or cuneate, often with few, large lobes, the margins crenate, plane; *veins* extending to or nearly to the margin, terminating in a shallow sinus, the ends slightly enlarged to clavate; *border* narrow, clear, 1–3 rows of elongated cells, those along the edge usually bulging at the apical end, those at the apex about as broad as long. *Sporangia* mostly on the penultimate veins, usually in a discrete submarginal band, the stalk of 1 or 2 tiers of clear cells subtending the capsule, the annulus of 17–23 indurated cells. *Spores* usually deep brown or slightly lighter, the proximal face with prominent ridges sometimes forming a reticulum adjacent to the triradiate scar, equatorial flange narrow to moderately broad the angles not projecting, the distal face smooth within the central areola.

Eriosorus Orbignyanus is similar to *E. flexuosus* in the scrambling habit of the leaves. Both species apparently were collected at Yuracares, Bolivia, by D'Orbigny. There are several differences between them, particularly in the shape and the division of the lamina, the spores and the orientation of the pinnules, suggesting that the scrambling habit may be a secondary character which was independently developed in the two species. The orbicular form of the ultimate segments and position of the sporangia in submarginal bands are also characteristic of *E. Wurdackii*. The larger guard cells in *E. Orbignyanus*, shown in Fig. 31f, may reflect a different ploidy level than those of *E. Wurdackii* (Fig. 30g). *Eriosorus Orbignyanus* is known only from fragmentary portions of the lamina, and it is difficult to reconstruct the complete leaves. The rhizomes are lacking in all collections but it is noted in the label data of one collection that they are embedded in mosses. The indument of the rhizome, used for indicating relationships in other species, is probably composed of unspecialized trichomes, similar to those found in *E. Wurdackii*.

D'Orbigny's collection 299 from Yuracarés includes some fertile pinnae and has been chosen to typify the species, rather than his collection 174, which seems to be completely sterile.

Scandent or scrambling on brush, rhizomes in sphagnum. Colombia to Bolivia, at 1400–3800 m.

ADDITIONAL SPECIMENS EXAMINED: **Colómbia. Santander:** Cerro Armas, *Haught 1961* (GH, US). **Antioquia:** Tabor, *Kalbreyer 1365* (B, K, NY-frag.). **Narino:** between Santa Lucia and Pasto, 3800 m., *Stübel 264* (B); 3 km. above Sachamate, *Ewan 16676* (GH, NO, S, US). **Ecuador. Azuay:** Cuenca, *Pearce 306* (K). **Peru.** July 5, 1910, *Markham* (K). **Huánuco:** s. of Monson, *Weberbauer 3514* (B, BM). **Junín:** Porvenir, *Killip & Smith 25947* (NY, US). **Cuzco:** Chaupimayo, *Bües 1949, 1950* (US); ca. Hacienda Luisiana, Prov. La Convención, *T. R. Dudley 11240* (GH); **Bolivia.** *Bang 2238* (B, BM, GH, K, NY, US, W), *2599* (K, NY, US). **La Paz:** Yungas, *Rusby 129*, in part *128* (US); Cargadira, *R. S. Williams 1111* (BM), Paradiso, *1248* (GH, NY, US). **Cochabamba:** Incachaca, *Brooke 6768* (BM).



MAP 16–19. MAP 16, *Eriosorus Orbignyanus*, dot; *E. Wurdackii*, star. MAP 17, *E. insignis*. MAP 18, *E. Biardii*. MAP 19, *E. Ewanii*.

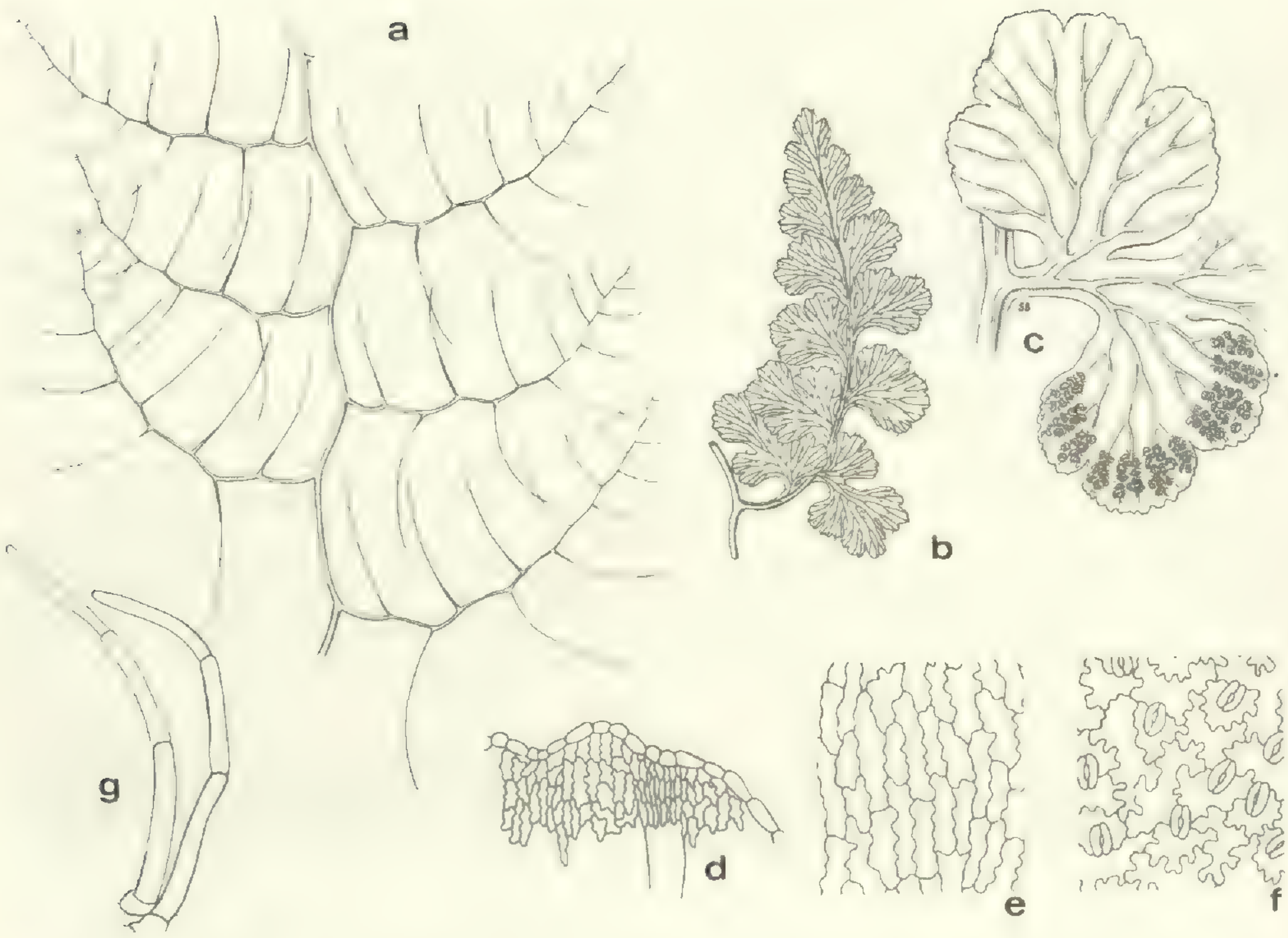


FIG. 31. *Eriosorus Orbignyianus:* a, diagram of pinna rachises and rachis from apical portion of a large leaf, × 1/3, *Ewan 16676* (US); b, tertiary segment with veins, × 2/3, *Bües 1950* (US); c, two ultimate segments with veins, one with sporangia in a submarginal band, × 2–2/3; d, margin with vein end; e, f epidermis, e upper epidermis, f lower epidermis; g, lamina trichomes from upper surface, all × 40, *Ewan 16676* (US).

21. **Eriosorus insignis** (Kuhn) A. F. Tryon, comb. nov.

FIG. 32, MAP 17

Gymnogramma insignis Mett. ex Kuhn, Linnaea 36:70. 1869. TYPE: *St. Hilaire,* Serra Negra, at border of Rio de Janeiro and Minas Gerais B!, photo GH; isotypes: *St. Hilaire* Cat. B'72 P!, photo GH, Cat. B'458 P!. The holotype at Berlin consists of mounted leaf fragments, some packet material, and a description of the species, all from the Mettenius Herbarium. On the same sheet there is a pencil sketch of part of the lamina and the printed description of *Psilogramme insignis* from Kuhn's herbarium. This material, upon which the description of *G. insignis* is based, appears to be fragments from the larger specimen at Paris collected by St. Hilaire.

Neurogramma scandens Fée, Crypt. Vasc. Brés. 1:263. 1869, 2:39, t. 92. 1873. TYPE: *Glaziou* 3552, Brazil, Serra os Orgaos, Aug. 7, 1869 P! photo GH; isotypes: K!, NY-frag. ex K!, P!, photo GH, US. In the second volume, *Glaziou* 5321 is also cited and there is an excellent illustration of the specimen.

Gymnogramma scandens (Fée) Bak. Jour. Linn. Soc. 14:25. 1873.

Psilogramme dubia Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 337. 1882. TYPE: *Glaziou* 5321, Brazil B, NY-frag. ex B!; isotype: P!

Psilogramme insignis Kuhn, op. cit. 337. 1882.

Gymnogramma dubia (Kuhn) Bak. Ann. Bot. 5:485. 1891.

Eriosorus Feei Copel. Gen. Fil. 58. 1947. Based on *Neurogramma scandens* Fée.

Rhizome elongate, repent, the internodes short, ca. 0.5–4.0 mm. in diameter, the trichomes or bristles rigid, appressed, deep brown to black, at the base 1–6 cells wide, 1 or 2 cells thick, the apical cell globose. *Leaves* scrambling, 30–82 cm. long (the longest incomplete). *Petiole* subterete near the rhizome, plane or channeled on the upper surface at the apex, castaneous or atropurpureous, as long as to 3 times longer than the lamina, sparsely to densely pubescent, the trichomes rigid, erect, clear to brown or bicolorous, the apical cell usually globose. *Lamina* elongate-triangular, the base usually slightly broader than the central portion, the apex acuminate, 3-pinnate, 23–50 cm. long, 8–18 cm. wide, determinate, the apical bud small, slightly pubescent. *Rachis* fractiflex, the upper surface channeled, atropurpureous or castaneous, slightly to densely pubescent, especially in the axils of the pinnae, the trichomes tan, brown or bicolorous, the apical cell globose. *Pinnae* at right angles to the rachis or sometimes descending at an angle greater than 90°, forming an arc with the apex ascending, elongate-triangular, the basiscopic side, slightly larger, 1.5–8.0 cm. long, 1–4 cm. wide, herbaceous to coriaceous; *upper surface* moderately to sparsely pubescent, the trichomes rigid, brown, or patent, clear or tan, the apical cell elongate or globose; *lower surface* more densely pubescent along the veins, the trichomes similar to those above; *stalk* 5–20 mm. long, sulcate, sometimes with decurent lamina tissue; *pinnules* ovate; *ultimate segments* orbicular or ovate with several shallow lobes, the margins crenate, usually plane; *veins* extending to or nearly to margins, terminating in a shallow sinus, slightly enlarged or clavate; *border* narrow, clear with 1–3 rows of elongate cells, those along the edge bulging, at the vein end irregular, about as long as broad. *Sporangia* mostly on the ultimate and penultimate veins, somewhat localized on the distal portion of the segments, the stalk of 1 or 2 tiers of clear cells, the annulus of 19–20 indurated cells. *Spores* deep brown, the proximal face with narrow ridges parallel to the triradiate scar, the equatorial flange narrow, the 3 angles not projecting, the distal face smooth within the central areola or with a few, coarse tubercles.

The large scandent leaves of these collections show considerable variation in the division of the pinnae and pinnule shape but are more uniform in details of the venation, spores and indument. The collection of *Santos Lima 417* has especially robust leaves with coarsely lobed pinnules. The cells of the upper epidermis are larger than those of other collections and have slightly undulate walls. The epidermal cell patterns from several collections, in Fig. 32, show considerable variation in size and probably reflect different ploidy levels. Those from the type collection of St. Hilaire are smaller than those of the Santos Lima collection.

The scandent, fractiflex leaves with descending pinnae, orbicular ultimate segments and dark spores suggest that *Eriosorus insignis* is closer to the Andean species, *E. Orbignyanus* and *E. Wurdackii*, than it is to the other Brazilian species, *E. myriophyllus* or *E. Biardii*. The more complex scrambling leaves and broad bristle-like rhizome indument indicate that the species represents

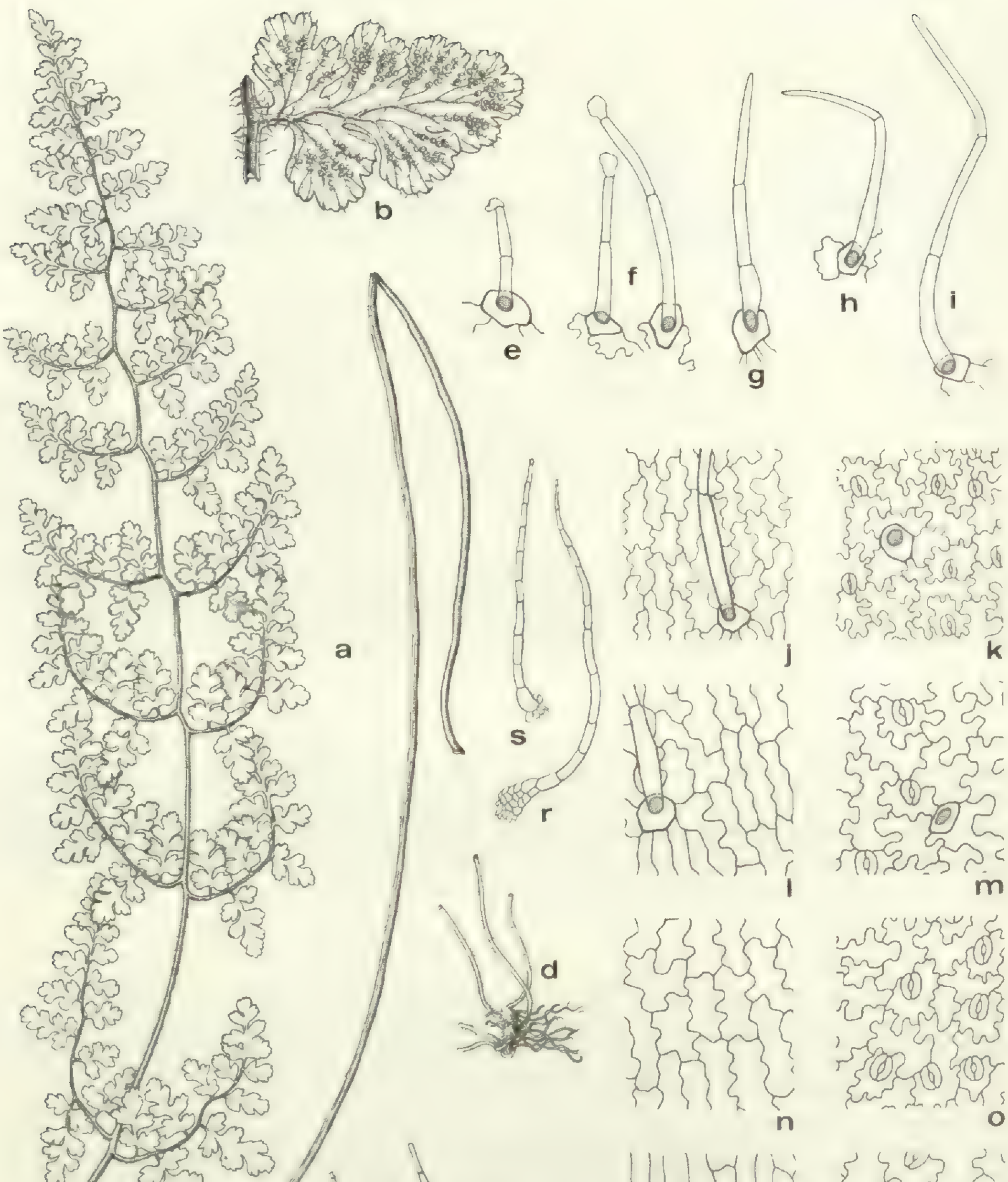


FIG. 32. *Eriosorus insignis:* a, leaf, × 1/3; b, pinnule, × 1–1/3; c, margin with vein ends and glandular trichomes on upper surface, × 20, all *St. Hilaire B' 72* (P); d, rhizome from small plant, × 1/3, *St. Hilaire B' 458* (P); e–i, lamina trichomes, × 40; e,g,i, upper surface; f,h, lower surface; e,f, *Tryon & Tryon 6701* (GH); g,h, *Silveira 462* (R); i, *St. Hilaire C72* (P); j–q, epidermal cells, the basal cells of trichomes darker, × 40; j,l,n, p, upper surface; k,m,o,q, lower surface; j,k, *St. Hilaire C72* (P); l,m, *Glaziou 3552* (P); n,o, *Tryon & Tryon 6701* (GH); p,q, *Santos Lima 417* (RB); r,s, rhizome bristles with few elongate rhizome cells at base, × 10; r, *St. Hilaire C458* (P); s, *Silveira 462* (R).

a fairly specialized one in the genus. It is exceedingly rare on Mt. Itatiaia where I found a single colony of a few plants on the planalto. They were in a moist crevice at the base of a large boulder apparently protected from the periodic burning of this high, rocky grassland.

Rare, in moist, shaded places at edge of boulders, or in caves. Eastern Brazil, at 1000–2300 m.

ADDITIONAL SPECIMENS EXAMINEDS **Brazil. Minas Gerais:** Serra da Caraça, *Alvaro Silveira 462* (P, R); Serra de Tbitipoca, *Schwacke 12310* (P, R). **Rio de Janeiro:** Therezopolis, *Glaziou 89*, April 1868 (R); Frade de Machai, *Brade 15802* (BM, G, NY, RB); Alto do Desingano, Sta. Magdalena, *Santos Lima & Brade 13151* (BM, RB); Serra Norte-Vermelho, Sta. Magdalena, *Santos Lima 417* (RB); Itatiaia, w. face of Pedra Assentada, *Tryon & Tryon 6701* (GH). **Sao Paulo:** Campos de Jordão, *Campos Porto 3108* (BM, RB).

22. **Eriosorus flexuosus** (HBK.) Copel. Gen. Fil. 58. 1947

Rhizome repent, with short internodes, ca. 4–8 mm. in diameter with rigid, usually appressed, lustrous deep brown to black trichomes, bristles, or rarely tan scales, at or near the base 1–11 cells wide, 1–3 cells thick, the apical cell usually elongate, sometimes globose. *Leaves* scrambling or scandent on other vegetation, sometimes exceeding 4 m. in length, erect in young, rarely in older plants. *Petiole* subterete or elliptical, atropurpureous to castaneous, at the base lighter, usually tan above, channeled, ca. 1/3 or 1/4 as long as the lamina, often nearly glabrous or with sparse to moderately dense pubescence, the trichomes rigid or crispate, tan to deep brown, with the apical cell elongate, rarely globose, glandular. *Lamina* elongate with the pinnae oriented in several planes, the central ones longer than those at the apex or base, 5- 6-pinnate, in the smallest fertile specimen 18 cm. long and 12 cm. wide, in the longest complete specimen 200 cm. long and 37 cm. wide (the basal pinnae usually deteriorated), indeterminate, the apical bud minute, slightly pubescent. *Rachis* fractiflex, the upper surface strongly channeled, straw colored near the apex, darker, castaneous to atropurpureous near the petiole, usually glabrous, sometimes with trichomes at the pinnae axils, or pubescent, the trichomes clear to light brown, the apical cell elongate, rarely globose, glandular. *Pinnae* usually ascending, departing at an angle less than 90°, oblong-acuminate or elongate-triangular (usually broadest near the rachis), the basiscopic side sometimes larger, 2–33 cm. long, 1–25 cm. wide, herbaceous, delicate or sometimes a more rigid texture; *upper surface* slightly pubescent, often sparsely so, to nearly glabrous, the trichomes clear or tan, the apical cell elongate or globose; *lower surface* sparsely pubescent, the trichomes often confined to the veins; *stalk* 3–10 mm. long, sulcate on the upper surface, with ridges continuous with those of the rachis, glabrous or pubescent; *pinnules* elongate-triangular or ovate; *ultimate segments* usually bifid, cuneate (variants often broadly cuneate) with slender lobes usually about as long as broad (variants often broadly cuneate), the margins retuse, rarely more strongly cleft, usually plane; *veins* extending to or sometimes ending short of the margin, not or slightly enlarged, rarely clavate; *border* narrow, clear or opaque, 1–3 rows of elongated cells, those along the edge bulging at the apical end, often protruding in an irregular

papillate border, those at the segment apex about as long as broad and strongly protruding. *Sporangia* along the ultimate and penultimate veins, rarely extending to the next division toward the rachis, the stalk short, 1–3 tiers on a cluster of cells adjacent to the vein, the annulus of 13–25 indurated cells. *Spores* tan or light brown, rarely darker, the proximal face with few irregular ridges adjacent to the triradiate scar, with narrow to moderately broad equatorial flange, the angles not or slightly projecting, the distal face usually with a smooth central areola or with few, coarse tubercles, sometimes aborted.

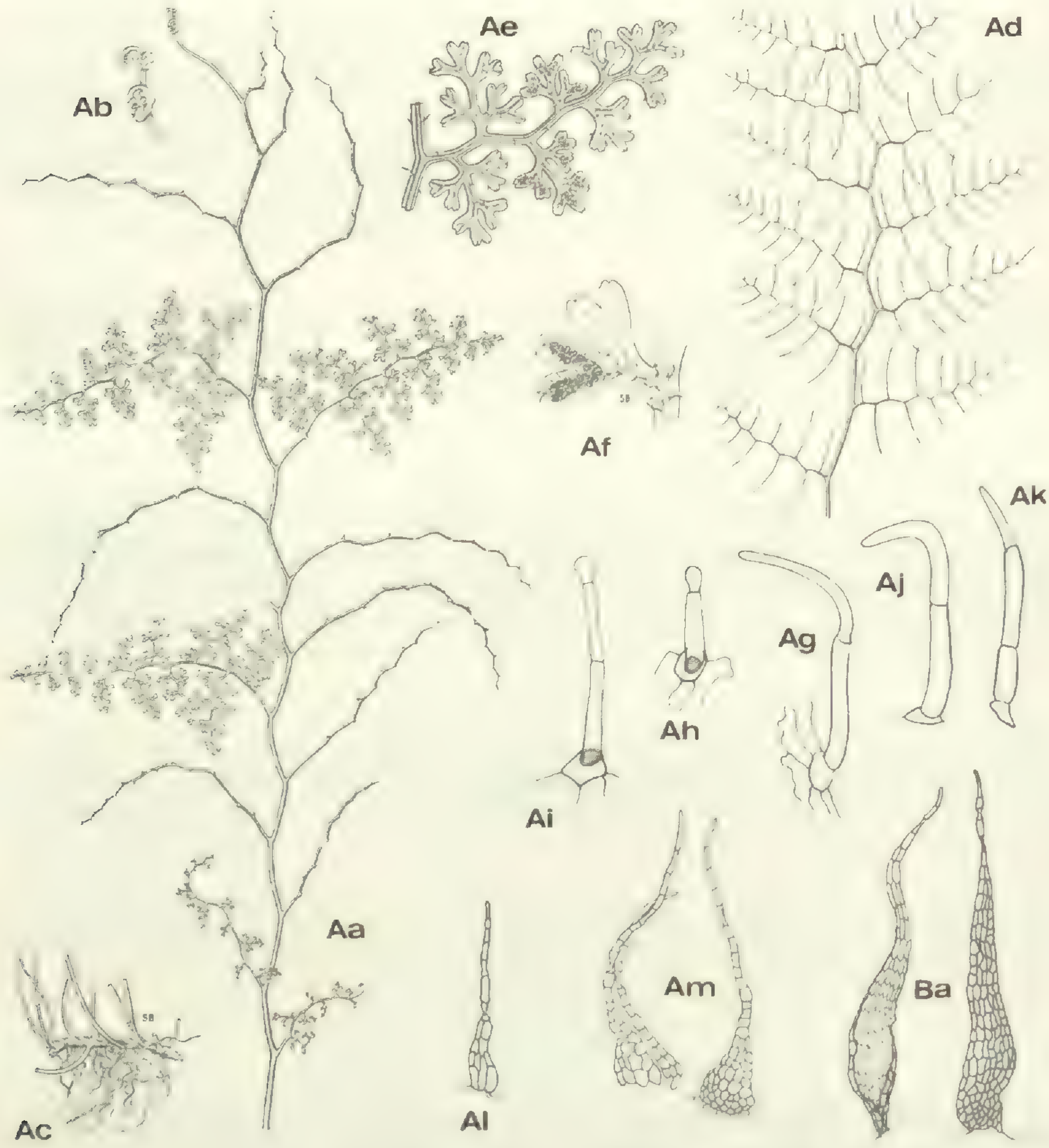


FIG. 33. *Eriosorus flexuosus:* Aa–Am var. *flexuosus:* Aa, lamina and petiole apex of a small leaf, with five pinnae in detail and rachis of others, × 1/3; Ab, apical bud, enlarged, *Tryon & Tryon 7004* (GH); Ac, rhizome, × 1/3, *Tryon & Tryon 6109* (GH); Ad, diagram of pinnae rachises and portion of the rachis, *Alston 6469* (GH); Ae, tertiary segment with veins and some sporangia, × 1, *Tryon & Tryon 7004* (GH); Af, two ultimate segments with veins, sporangia and trichomes on one, × 2–2/3, *Tryon & Tryon 6109* (GH); Ag–Ak, lamina trichomes (Ah,Ai, with apical cell glandular) × 40; Ag–Ai, upper surface; Aj, Ak, lower surface; Ag,Aj, *Humboldt & Bonpland* (P); Ah, *Killip & Smith 18195* (US); Ai, *Steyermark & Wurdack 789* (US); Ak–Am, rhizome bristles, × 10; Ak, Al, *Tryon & Tryon 6109* (GH); Am, *Alston 6469* (GH). Ba var. *galeanus:* rhizome scales, × 10, *Hinton 14221* (GH).

Eriosorus flexuosus has the most extensive distribution of the genus on the American continents. It ranges from southern Mexico to Bolivia, and occurs in eastern Brazil and in the Greater Antilles. It also has the greatest altitudinal range, occurring at 800 m. in southern Mexico and up to 4200 m. in the Cordillera Oriental of Colombia. It has been more frequently collected than other species because it is very conspicuous. The plants are scrambling or climbing on shrubby growth in the lower montane zone and in low woods bordering páramos. The leaves may attain more than four meters in length, and are usually fractiflex with the pinnae oriented in several planes. The ultimate segments are usually slender and bifurcate but may be broader and cuneate.

The collections included in the general citations represent only a portion of the material studied, and consist mainly of the most widely distributed collections. Several variants are included as examples of some of the main deviations from the usual pattern, particularly those which can be associated with other species. To a large extent, hybridization has been a factor in the production of variation. The putative hybrids involving *E. flexuosus* are treated by formula under the species they most closely resemble. They are also noted in each case under the treatment of the second parent.

The record of meiotic chromosome counts of 87 bivalents at meiosis reported here in *Eriosorus flexuosus* var. *flexuosus* from Costa Rica is interpreted as a hexaploid level and implies the existence of three lower chromosome levels. The hybrid with *E. Warscewiczii* from Volcán Poás is proposed on the basis of the associations of plants in the field and the cytological analyses of meiotic cells. There are ca. 174 chromosomes in these, mostly univalents as shown in Fig. 2g.

The new variety, *E. flexuosus* var. *galeanus*, known only from the Galeana district in Guerrero, Mexico, is the northernmost record for the genus. The plants are especially notable because they have true scales on the rhizome. These structures, shown in Fig. 33Ba, are several cells wide and may be somewhat thickened at the base, but are usually distinctly laminar above. The leaves are somewhat more pubescent than in var. *flexuosus*, but are generally similar to that variety in the form and division of the pinnae. For this reason they were not illustrated.

Eriosorus flexuosus represents one of the most derived species in the genus as is evident from the complexity of the leaves,

bristles and scales on the rhizome and light colored spores. Similarities with other species such as *E. Ewanii* and *E. Biardii* suggest that these species may be intermediates involving *E. flexuosus*. The large, scandent leaves of *E. flexuosus* are also similar to *E. glaberrimus*, but other differences in the spores and rhizome indument do not support a close relationship. The shape of the ultimate segments, their borders and vein ends, as well as the broad bristles on the rhizome and light spores are similar to *E. hirtus*. The more complex leaf form of *E. flexuosus* has probably evolved from a simpler one similar to that of *E. hirtus*.

KEY TO THE VARIETIES OF ERIOSORUS FLEXUOSUS

Rhizome with lustrous deep brown to black trichomes or bristles; leaves scandent or scrambling and herbaceous or more rigid in texture . . . . . 22a. *E. flexuosus* var. *flexuosus*

Rhizome with light brown or tan scales, leaves erect, and delicate herbaceous in texture . . . . . 22b. *E. flexuosus* var. *galeanus*.

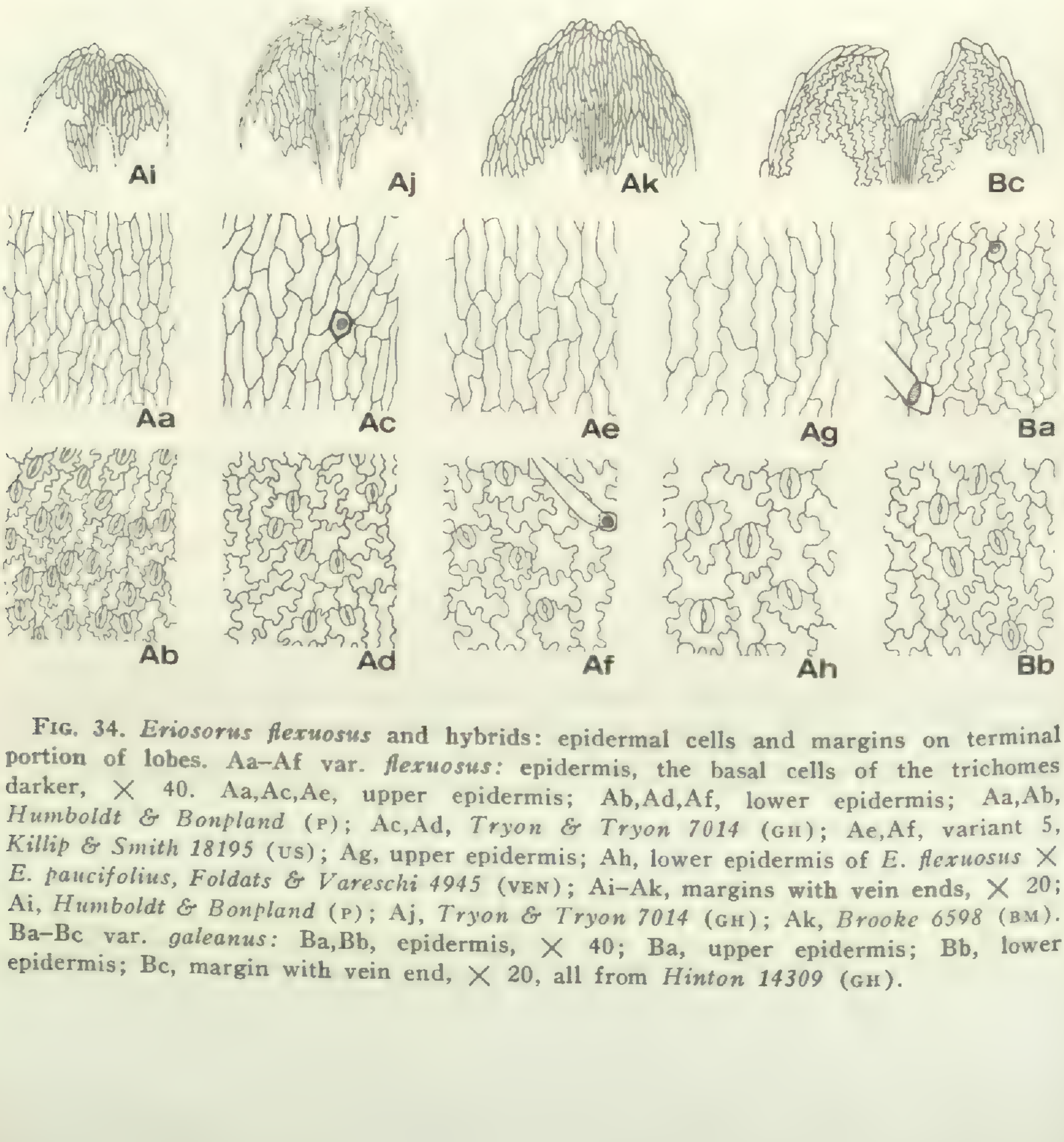


FIG. 34. *Eriosorus flexuosus* and hybrids: epidermal cells and margins on terminal portion of lobes. Aa–Af var. *flexuosus:* epidermis, the basal cells of the trichomes darker, × 40. Aa,Ac,Ae, upper epidermis; Ab,Ad,Af, lower epidermis; Aa,Ab, *Humboldt & Bonpland* (P); Ac,Ad, *Tryon & Tryon 7014* (GH); Ae,Af, variant 5, *Killip & Smith 18195* (US); Ag, upper epidermis; Ah, lower epidermis of *E. flexuosus* × *E. paucifolius, Foldats & Vareschi 4945* (VEN); Ai–Ak, margins with vein ends, × 20; Ai, *Humboldt & Bonpland* (P); Aj, *Tryon & Tryon 7014* (GH); Ak, *Brooke 6598* (BM). Ba–Bc var. *galeanus:* Ba,Bb, epidermis, × 40; Ba, upper epidermis; Bb, lower epidermis; Bc, margin with vein end, × 20, all from *Hinton 14309* (GH).

22a. **Eriosorus flexuosus** var. **flexuosus**

FIG. 33A, 34A, MAP 20

Gymnogramma flexuosus Desv. Ges. Naturf. Freunde Berlin Mag. **5**:306. 1811. TYPE: Am. Aequin. Herb. Desv. P! photo GH.

Grammitis flexuosa HBK. Nov. Gen. et Sp. **1**:4 (Fol. ed.) 1816, **1**:5 (4° ed.) 1816, not Humb. & Bonpl. Aequin. **2**:167. 1809, as sometimes cited in error, see Hook. Sp. Fil. **5**:129. 1864. TYPE: Venezuela, near Caracas, *Humboldt & Bonpland*, Herb. Kunth ex Herb. Humboldt, B! photo GH; isotypes: 3 sheets P! photo GH: leg. *Bonpland*, Herb. Mett. B!

Cryptogramma retrofracta Grev. & Hook. Bot. Misc. 3:385, t. 112. 1833. TYPE: *Jameson*, Ecuador, near Molleturo E! photo GH.

Gymnogramma refracta Kze. ex Kl. Linnaea **20**:410. 1847. TYPE: *Moritz* 359, Venezuela, Sierra Nevada, B! photos GH, US; isotypes B! photos GH, US; BM! photo GH; P! photo GH; fragments F! US!

Gymnogramma Ruiziana Kze. ex Kl. Linnaea **20**:410. 1847. TYPE: *Ruiz 74*, Peru, Prov. Panatahuarum, B! photo GH.

Anogramma refracta (Kze. ex Kl.) Fée, Gen. Fil. 184. 1852.

Gymnogramma retrofracta Kze. ex Mett. Fil. Lech. **1**:10. 1856. nom. superfl.; *G. refracta* Kl. is cited as a synonym.

Gymnogramma retrofracta (Hook. & Grev.) Hook. Sp. Fil. **5**:129. 1864, in synon.

Gymnogramma recurvata Karst. Fl. Columbiae **2**:165, t. 187, f. 1. 1869. TYPE: *Karsten*, Colombia, prope Chiquinquira, LE.

Psilogramme flexuosa (HBK.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 339. 1882.

Gymnogramma haematodes Christ, Bull. Herb. Boss. II, **4**:1097. 1904. TYPE: *Tonduz 10713*, Costa Rica, Volcán du Poás, Dec. 1896, chosen by Maxon, P! photo GH; isotype US!; paratypes: *Pittier 1936*, Costa Rica, Forêts du Barba, P! photo GH; isoparatype: US!; *Wercklé s.n.* Costa Rica.

Gymnogramma flexuosa var. *linearis* Christ, Bull. Herb. Boiss. II, **4**:1096. 1904. TYPE: *Tonduz 12796*, Costa Rica, Las Vueltas, Tucurrique, P!; isotype: G!

Gymnogramma flexuosa var. *peruviana* Hieron. Hedwigia **48**:220. 1909. TYPE: *Stübel 1055*, Peru, Dept. Amazonas, Cuesta de Lejia, prope Molinobamba, B! photo GH.

Psilogramme haematodes (Christ) Maxon, Bull. Torrey Bot. Club **42**:84. 1915.

Psilogramme refracta (Kze. ex Kl.) Maxon, op. cit. 85. 1915.

Psilogramme villosula Maxon, op. cit. 83. 1915. TYPE: *Pittier 10502*, Costa Rica, Cerro de Las Vueltas, Jan. 1897, US! isotypes P!, US!

Gymnogramma villosula (Maxon) C. Chr. Ind. Fil. Suppl. Prélim. 19. 1917.

Gymnogramma platytrichia C. Chr. Svensk. Vet. Akad. Handl. **16**:58. 1937. TYPE: *Ekman 10657*, Haiti, Massif de la Hotte, s!, isotypes B!, US!

Eriosorus villosulus (Maxon) Scamman, Contrib. Gray Herb. 191. 1–88. 1962.

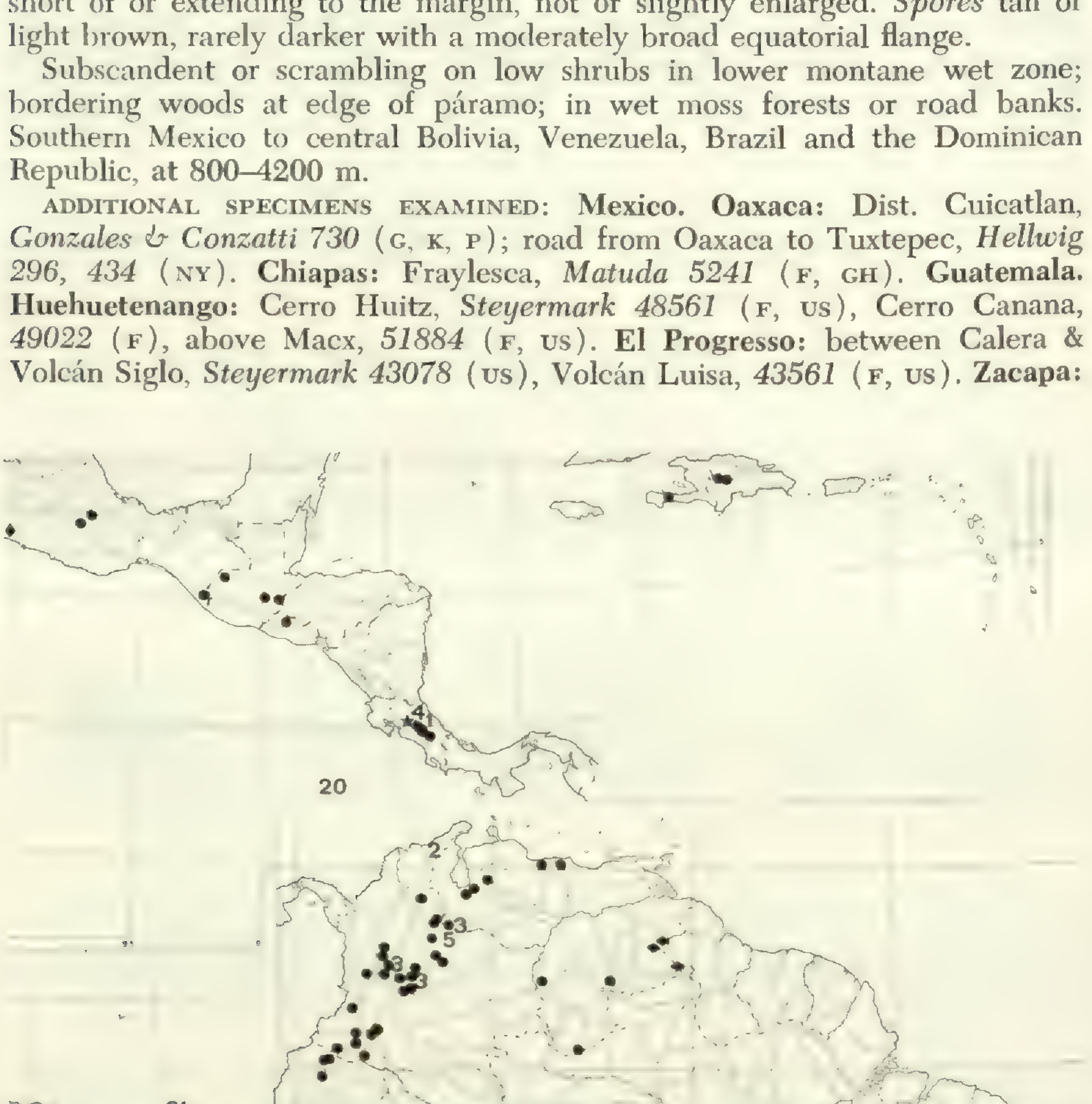
Eriosorus retrofractus (Kze. ex Mett.) Crabbe, Brit. Fern Gaz. **9**:315, 1967 is illegitimate as it is based on a superflous name.

Rhizome with rigid, usually appressed, lustrous, deep brown or black trichomes, or bristles, sometimes broader, scale-like, darker than the rhizome surface, at or near the base 1–10 cells wide, 1–3 cells thick, the apical cell elongate or globose. *Leaves* scrambling or scandent, elongate, the pinnae

oriented in several planes, the central ones longer than those at apex or base, near the apex the lateral pinnae about as long as or longer than the central member. *Rachis* glabrous or slightly pubescent. *Pinnae* ascending and spreading, not appressed to the rachis, herbaceous, often rigid, with sparse trichomes on both surfaces or glabrous above, rarely glandular; *veins* ending short of or extending to the margin, not or slightly enlarged. *Spores* tan or light brown, rarely darker with a moderately broad equatorial flange.

Subscandent or scrambling on low shrubs in lower montane wet zone; bordering woods at edge of páramo; in wet moss forests or road banks. Southern Mexico to central Bolivia, Venezuela, Brazil and the Dominican Republic, at 800–4200 m.

ADDITIONAL SPECIMENS EXAMINED: **Mexico. Oaxaca:** Dist. Cuicatlan, *Gonzales & Conzatti 730* (G, K, P); road from Oaxaca to Tuxtepec, *Hellwig 296, 434* (NY). **Chiapas:** Fraylesca, *Matuda 5241* (F, GH). **Guatemala. Huehuetenango:** Cerro Huitz, *Steyermark 48561* (F, US), Cerro Canana, *49022* (F), above Macx, *51884* (F, US). **El Progresso:** between Calera & Volcán Siglo, *Steyermark 43078* (US), Volcán Luisa, *43561* (F, US). **Zacapa:**



MAP 20, 21. MAP 20, *Eriosorus flexuosus* var. *flexuosus,* dot; variants 1–6 as cited in text; hybrid, *E. flexuosus* var. *flexuosus* × *E. Warscewiczii,* star; hybrid, *E. flexuosus* var. *flexuosus* × *E. paucifolius,* rhomb.; *E. flexuosus* var. *galeannus,* diamond. MAP 21, *E. glaberrimus,* dot; hybrid, *E. glaberrimus* × *E. congestus,* star.

Volcán Gemelos, *Steyermark 43301* (F, US). **El Salvador. Chalatenango:** Los Esemiles, *Tucker 1120* (F, G, K, MICH, US). **Costa Rica. Alajuela:** upper slopes Póas, *Scamman 7627* (GH); *J. D. Smith 6931* (B, BM, F, G, GH, K, US); *Tryon & Tryon 7001, 7004, 7010, 7012, 7014, 7016* (GH). **San José:** between El Empalme & Villa Mills, *Cruz 74* (GH); Cerro de la Muerte, *Tryon & Tryon 7051* (GH); La Chonta, *Scamman & Holdridge 7925* (GH). **Cartago:** Volcán de Turrialba, *Standley 35024* (US); Irazú, *J. D. Smith 4999* (K, US). **Colombia. Norte de Santander:** Páramo de Fontibón, *Alston 7145* (BM, GH); *Cuatrecasas & Garcia Barriga 10090* (COL, F, GH, US); Páramo de Tamá, *Cuatrecasas* et al. *12675* (GH); Páramo de Romeral, *Killip & Smith 18678* (GH, NY, US), Páramo de Santurban *19607* (COL, GH, NY, US). **Santander:** n. of Velez, *Ewan 15668* (GH, NO, US); Pamplona, *Kalbreyer 1130* (B, K); Páramo de Romeral, *Killip & Smith 18506* (GH, NY, P, US). **Boyacá:** Páramo de Belén, *Barclay & Juajibioy 7660* (GH); Páramo de Albarracín, *Murillo 801* (GH). **Cundinamarca:** Usaquen, *Alston 7465* (BM, GH); Montserrate, *Ewan 16916* (NO, US); *Little & Little 9448* (COL, US); La Vega-Facatativa, *Haught 6144* (F, NY, S, US); Bogotá, *Lindig 34* (B, GH, K, P); *Schiefer 517* (GH); Páramo de Guasca, *Tryon & Tryon 5926* (GH), 7 km. sw. Sibate, *6109* (GH). **Tolima:** Volcancitos, *Killip & Hazen 9490* (GH, US). **Huila:** Comissaría de Caquetá, *Cuatrecasas 8434* (US). **Bolívar:** Antizales, *Pennell 4457* (F, GH, K, NY, US). **Antioquia:** St. Elena, *Archer 1811* (C, US); El Santuario, *Daniel 15, 543* (US), Yarumal, *39* (F, US), Sonsón, *245* (US), Medellín, *287* (US), Cerro de la Vieja, *1726* (US); Las Palmas, *Hodge 6548, 6627* (GH). **Caldas:** Termales, *Tryon & Tryon 6133* (GH). **Valle:** Hoya del Rio Cali, *Cuatrecasas 21604* (F, US). **Cauca:** Puracé, *Tryon & Tryon 5965* (GH); Páramo de las Papas,*Idrobo* et al. *3031* (COL, GH); San Antonio,*Pennell 7367* (GH, NY, US). **Narino:** Pasto, *Jameson 476* (US); Volcán de Cumbal, *Ewan 16152* (NO, US). **Putumayo:** El Encano, *Porter 1076* (GH). **Ecuador. Carchi:** Volcán Chile, *Wiggins 10611* (NY). **Imbabura:** Coracachi, *Acosta Solis 8275* (F). **Pichincha:** Quito, *Sodiro* 9/81 (P, US). **Canar:** Azogues, *Camp E1785* (NY, US). **Azuay:** s. of Cuenca, *Camp E3913* (F, G, GH, K, NY, VEN), Sevilla de Oro, *E4617* (NY, US). **El Oro:** Zaruma, *R. Espinosa E2133* (GH, NY). **Santiago-Zamora:** between Sevilla de Oro and Mendez, *Camp E1616* (NY, US). **Loja:** se. of Loja, *Espinosa E1570* (GH, NY). **Peru. Cajamarca:** La Pucarilla, *López & Sagástegui 5458* (GH). **Amazonas:** below Chachapoyas, *Wurdack 777* (GH). **Junín:** Vitoc, *Martinet 1499* (P). **Huánuco:** Mito, *Macbride & Featherstone 1829* (F, G, GH, US, W); Carpish, *Ferreyra 9421, 10011* (GH); *Tryon & Tryon 5323* (GH). **Huancavelica:** e. of Surcubamba, *Stork & Horton 10393* (F, G, GH, K). **Cuzco:** Cerro de Cusilluyoc, *Pennell 13941* (F, GH, NY); Pillahuata, *Vargas 16754* (GH). **Puno:** San Gavan, *Lechler 2247* (B, E, G, K, P, W); entre Ayapata y Kahualluyoc, *Vargas 10750* (GH). **Bolivia.** Yorocares, *D'Orbigny 298* (B, G, P, W). **La Paz:** Unduavi, *Brooke 6598* (BM, F, G, NY, S); Yungas, *Bang 661* (B, BM, E, GH, K, NY, W); Sorata, *Mandon 1551* (BM, G, GH, NY, K, P, S-PA, W). **Cochabamba:** Tablas, *Herzog 2170* (B, S, US); Incacha-Chusi, *Steinbach 9250* (E, F, GH, NY, S-PA, US). **Venezuela. Sucre:** Cerro Turumuquire, *Steyermark 62654* (VEN), *62655a* (F, US). **Bolívar:** Ilu-Tepui, *Maguire 33409* (US); Meseta de Jáua, *Steyermark 97974* (GH); Chimantá Massif, *Steyermark & Wurdack 528* (US). **Amazonas:** Cerro de la Neblina, *Maguire* et al. *36942* (US); Cerro Sipapo, *Maguire & Politi 27747* (US). **Miranda:** Pico Naiguatá, *Pittier 6263* (B, NY). **Aragua:** Colonia Tovar, *Fendler 300* (G, GH, K, P, US); *Moritz 439* (B, P). **Lara-Trujillo:** Páramo de los Nepes, *Barclay & Juajibioy 10285* (GH). **Trujillo:** above Bocono, *Alston 6469* (BM, GH). **Mérida:** Sierra Nevada, *Funck & Schlim 1110* (E, G, HBG, P, W); Páramo Monsalves, *Vareschi 2261*

(VEN). **Táchira:** s. of Alquitrana, *Steyermark* et al. *101061* (GH). **British Guiana.** Roraima, *im Thurn 159* (K, US); Jenman, 1894 (E, NY). **Brazil. Espírito Santo:** Cerro Batatal, *Glaziou 15739* (B, C, G, K, P). **Dominican Republic. La Vega:** Loma Rosilla, *Fuertes 1784* (E, G, GH, K, P, US, W); se. of Valle Nuevo, *Gastony 721, 737* (GH). **Santiago:** Monción, *Ekman 12851* (B, C, K, S, US).

The following series of six variants is cited separately from the main citations to emphasize the kinds of variation within this species. It is possible that they include hybrids and lower chromosome number polyploid elements in the species. They are most readily distinguished by densely pubescent or glandular leaves with shallow lobes and cuneate segments. The series is arranged in two groups based on leaf indument. Specimens included under numbers 2–6 in the series are mostly fragmentary portions, apparently from large leaves. These are without petiole or rhizome and therefore are especially difficult to identify.

VARIANTS WITH PUBESCENT LEAVES AND USUALLY SIMPLE TRICHOMES

1. In his treatment of *Psilogramme* Maxon described *P. villosula* and distinguished it from closely related species on the basis of copiously short-villose leaves. He cited only the type. This and other collections noted below can be distinguished by this character as well as somewhat broader ultimate segments than are usual for var. *flexuosus*. The Pittier collection has both glands and trichomes on the leaves, and Maxon indicated that it was probably another species. It is likely that *E. congestus*, which has dense pubescence on the leaves, and is in the same range, may be implicated if hybridization has occurred. **Costa Rica. San José:** El Páramo region du General, *Pittier 10452* (US); Cerro de las Vueltas, *Standley & Valerio 43563* (MICH, US); San Isidro de El General, *Scamman 6076* (GH); *Williams* et al. *24403* (F); Cord. Talamanca, *Weber 6228* (GH); *Williams* et al. *28851* (C, F).

2. Specimens from the Santa Marta ranges in northern Colombia are unusually variable and have compact, cuneate ultimate segments. *Eriosorus hispidulus*, which has broadly cuneate segments is also there and may be involved if hybridization has occurred. **Colombia. Magdalena:** Mundo Nuevo, *Apolinair 618* (GH); Cerro Huemado, *Giacometto 18, 43* (GH); Río Hacha, *Schlim 845* (G, K, P); San Lorenzo Ridge, *H. H. Smith 2214* (F, GH, K, NY, S-PA, US).

3. Specimens with broadly cuneate, shallowly lobed ultimate segments and with deep brown spores are possibly intermediates derived by hybridization with other species. They are widely distributed and occur within the ranges of several taxa. As field data on species associations become available the status of this material may be clarified. **Venezuela. Táchira:** Páramo de Tamá, *Steyermark 17314* (F, GH); *Steyermark & Dunsterville 98582* (GH). **Colombia. Norte de Santander:** Páramo del Hatico, *Killip & Smith 20628* (GH, NY, US). **Antioquia:** Alto Capiro, *Ewan 15763* (NO, US). **Cundinamarca:** San Miguel, *Cuatrecasas & Jarmillo 12037* (US). **Cauca:** Mount el Derrumbo, *Pennell 7508* (GH, NY, US). **Ecuador. Azuay:** Sevilla de Oro, *Camp E4770* (NY, US). **Peru. Cajamarca:** Socota, *Stork & Horton 10132* (F, K). **Bolivia.** Río Juntas, *O. Kuntze*, April 1892 (B, NY).

VARIANTS WITH GLANDULAR LEAVES

4. The material cited below differs from the strongly scandent specimens

under Variant 1 because of its more erect habit. The more compact and densely glandular leaves suggest that *E. congestus* may be involved if hybridization has occurred. **Costa Rica. San José:** n. of San Isidro del General, *Alfonso Jimenez 2990* (F, GH).

5. The plants of the cited collection have well formed tan spores and the lamina texture is more delicate than other variants from Colombia. Epidermal cell size and patterns, as shown in Fig. 34g, h, are quite uniform. **Colombia. Santander:** Páramo de las Puentas, *Killip & Smith 18195* (BM, COL, GH, NY, S, US).

6. The following collection is extremely fragmented but quite distinct in the broad, cuneate shape of the ultimate segments. *Eriosorus hirtus* var. *glandulosus* occurs in the same department in Ecuador as this variant. A putative hybrid with *E. flexuosus* is proposed under that taxon. This collection differs from that in its scandent habit. **Ecuador. Loja:** *André 4514* (F, GH, K, NY).

PUTATIVE HYBRIDS INVOLVING ERIOSORUS FLEXUOSUS

Eriosorus flexuosus var. flexuosus × Eriosorus Warscewiczii

Eriosorus Warscewiczii is frequent at the high altitudes near the crater on Volcán Poás. Somewhat lower, in the cutover forests, *E. flexuosus* var. *flexuosus* is very abundant. The former occurs here, less commonly, and there are also hybrids of it with var. *flexuosus*. The hybrids most closely resemble var. *flexuosus* in leaf form, but in the strongly cuneate shape of the ultimate segments and dark spore color they resemble *E. Warscewiczii*. The spores are largely irregular and meiotic cells have 174 chromosomes which are mostly univalents, but some pairs and multivalents occur also. Both parents from this locality have 87 completely paired bivalents at meiosis. A somewhat smaller plant from the same population with broader pinnules and irregular spores has been designated by the letter *a* under the same number. **Costa Rica. Alajuela:** along road, below Poás crater, in turfy humus, 2500 m., *Tryon & Tryon 7011, 7011a* (GH).

Eriosorus flexuosus var. flexuosus × Eriosorus paucifolius

Eriosorus Lasseri Vareschi, Acta Bot. Ven. 1:94, f. 6. 1966. TYPE: *Vareschi & Foldats 4945*, Venezuela, Bolívar, Cerro Auyantepui, VEN (pinna fragments seen).

The material that I have examined of the type collection of *Eriosorus Lasseri* represents only two fragmentary portions of pinnae and a drawing of a "rhizome scale." This material consists of two elements. One most closely resembles *E. paucifolius* in its form and pinnule division and is eglandular. The other is glandular. Both are generally similar to more complete collections cited below, all of which have erect leaves with flexuose rachises. The fractiflex rachises and broad rhizome bristles of these putative hybrids clearly implicate *E. flexuosus*. *Eriosorus flexuosus* var. *flexuosus* occurs on the sandstone massifs in the state of Bolívar in Venezuela. *Eriosorus hispidulus* and *E. paucifolius* are also known from the massifs in Bolívar and either or possibly both may be involved in these hybrids. Although the second parent for these putative hybrids is not certain, *E. paucifolius* is proposed above on the basis of the dark spore color and glandularity

as well as its occurrence on the massifs in the state of Bolivar. **Venezuela. Bolívar:** Cerro Auyantepui, *Vareschi & Foldats 4857* (VEN); below El Liberator, *Steyermark 93983* (GH, VEN); Roraima, *Steyermark 58754* (F, US). **British Guiana.** Mt. Roraima, *McConnell & Quelch 629* (K, NY).

The large specimen cited below is much fragmented but the scandent leaves resemble *E. flexuosus*. It differs from the previous collections in having densely glandular leaves and a copious exudate on the glands. The guard cells in this collection are about twice as large as those of the Humboldt collection which represents the type of *E. flexuosus* from the vicinity of Caracas. **Venezuela. Bolívar:** Chimanta Massifs, *Steyermark & Wurdack 789* (US).

22b. **Eriosorus flexuosus** var. **galeanus** A. F. Tryon, var nov.

FIG. 33B, 34B, MAP 20

Rhizoma internodiis brevibus squamis vel setis pallide fuscis vel fulvis, lamina elongata plus minusve oblongata 4- vel 5-pinnata pinnis in planis 1 vel 2 dispositis apice acuminato indeterminato gemma plus minusve pubescenti, pinnae delicate herbaceae adaxialiter et abaxialiter trichomatibus sparsis, nervi ad marginem attingentes non vel leviter dilatati, sporae pallide fuscae.

TYPE: Mexico, Guerrero, Puerto Gallo, del Cerro Teotepec, August 11, 1964, *Rzedowski 18594* GH; isotype: NY.

Rhizome with lax, crispate, light brown or tan scales or thickened bristles, lighter than the rhizome surface, at or near the base 3–11 cells wide, 1–3 cells thick, the apical cell elongate. *Leaves* erect or scrambling, with pinnae oriented in 1 or 2 planes, the central or basal pinnae longest, the leaf apex acuminate. *Rachis* pubescent. *Pinnae* ascending and spreading, not appressed to the rachis, delicately herbaceous with sparse, clear trichomes on both surfaces; *veins* extending to the margin, not or slightly enlarged. *Spores* light brown with a narrow equatorial flange.

Several species of *Eriosorus* have rhizomes with bristles or thickened scale-like indument, but these plants have light colored, laminar scales. The basal portion is similar to the bristle or scale-like structures in var. *flexuosus*. The cells above the base form a broad lamella as illustrated in Fig. 33Ba. The leaves of var. *galeanus* are not illustrated as they are generally similar in detail to those of var. *flexuosus*. Field data accompanying the collections note the habit as "terestre" and "sobre los arbustos." I interpret this as terrestrial, scrambling on shrubs and, therefore, similar to the habit of var. *flexuosus*, but I have seen no collections of the latter north of Oaxaca. These plants of Guerrero represent the most northerly record for the genus and it would be of interest to know if they geographically replace var. *flexuosus* or grow in association with it. The Hinton collection lacks the rhizomes but it is included here because of the similarity of the light brown spores, pubescent rachises and the veins terminating at the segment margins.

The variety is named for the district Galeana, in the state of Guerrero, in which all of the collections have been made.

Terrestrial, sometimes scrambling on shrubs, growing between shrubs in oak and pine forest. Southwestern Mexico, at 2450–3025 m.

ADDITIONAL SPECIMENS EXAMINED: **Mexico. Guerrero:** Piedra Ancha, *Hinton 14221* (F, GH, US), Teotepec, *14309* (F, GH, US); Cerro Teotepec, 2 km. ne. del Campamento El Gallo, *Rzedowski & McVaugh 125* (NY).

23. **Eriosorus Ewanii** A. F. Tryon, spec. nov.

FIG. 35, MAP 19

Rhizoma plantae juvenilis internodiis longis trichomatibus fuscis ad basim cellulis 1–3 plerumque 1 latis, lamina elongata oblongo-trullata vel rhombica 4-pinnata pinnis in planis aliquot dispositis apice indeterminato gemma minuta glandulifera, rhachis fractiflexa atropurpurea vel castanea dense glandulifera, pinnae imbricatae valde ascendentes trullatae vel oblongo-rhombicae rigido-herbaceae adaxialiter et abaxialiter glandibus capitatis exudatiferis, pinnulae trullatae segmentis ultimis gracilibus bifidis profunde lobatis, nervi ad marginem attingentes plerumque dilatati extremis callosis incrassatis, sporae atrofuscae aliquando irregulares.

TYPE: Colombia, Nariño, n. slope of Volcan El Galeras, 3500 m. *Ewan 16316* GH; isotypes: NO, S, US.

Rhizome (of young plants) repent, the internodes elongate, ca. 2 mm. in diameter, the trichomes or bristles rigid, mostly appressed, golden to ruddy brown, at the base 1–3, usually 1 cell, the apical cell elongate. *Leaves* erect, or twining, 23–47 cm. long. *Petiole* terete, or subterete, atropurpureous or lighter, ca. less than half as long as the lamina, glandular, the glands similar to those of the rachis. *Lamina* elongate-trullate or -rhomboid, the pinnae oriented in more than one plane, the central ones often longest, 4-pinnate, 9–38 cm. long, 2–8 cm. wide, indeterminate, the apical bud minute, glandular. *Rachis* fractiflex, the upper surface strongly channeled, atropurpureous or castaneous, densely glandular, the glands with long, clear basal cells and globose, yellow apex. *Pinnae* ascending at an acute angle and appressed to the rachis, usually imbricate, elongate-ovate or -trullate (the pinnules adjacent to the rachis reduced), 2–8 cm. long, 1.0–3.5 cm. wide, rigid herbaceous; *upper surface* glandular, the globose apical cell of the glands covered with yellow or tan exudate; *lower surface* with similar, less dense indument; *stalk* 2–6 mm. long, sulcate on the upper surface, glandular; *pinnules* elongate-ovate; *ultimate segments* usually bifid, cuneate, with slender lobes, often longer than broad, the margins retuse or more strongly cleft, plane or sometimes enrolled; *veins* extending to the margin, dilated at ends forming a pad of thickened tissue in marginal sinus, or broadly clavate; *border* narow, clear, opaque, 1–3 rows of elongated cells, those at the vein end about as long as broad or longer and forming a thick cushion. *Sporangia* on the ultimate or penultimate vein the stalk short, of one tier or cluster of cells adjacent to the vein, the annulus of 17–24 indurated cells, often irregular. *Spores* deep brown, the proximal face with prominent ridges adjacent to the triradiate scar, the equatorial flange usually narrow, the angles prominently projecting, the distal face with coarse tubercles within the central areola, sometimes irregular or aborted.

The dense glandular indument and thickened vein ends are distinctive features of these plants. Their relationship to *E. flexuosus* is clearly shown by the general form of the lamina and ultimate segments. The oblique orientation of guard cells in the epidermis shown in Fig. 35f, the irregular sporangia and frequent aborted spores suggests that these plants may represent an intermediate involving *E. flexuosus* in some hybrid combination. The

collections are from páramos at high altitudes. The reduced form and glandular lamina of the specimens suggest possible connections with *Jamesonia*. Both *J. pulchra* and *J. cinnamomea* have been collected on Volcán El Galeras; the latter, with glands and dark spores, is close to *Eriosorus*. On the basis of the relatively wide distribution of these plants of *E. Ewanii* in southern Colombia it appears that they are effectively reproduced by spores.

It is a special pleasure to name this for Professor Joseph A. Ewan in recognition of his contributions to our knowledge of South American plants which has been greatly enriched by his collections and his particular interest in ferns.

Growing in tufts among low bushes, on páramo and upper páramo scrub. Southern Colombia, at 3400–3765 m.

ADDITIONAL SPECIMENS EXAMINED: **Colombia. Cauca:** Quebrada del Duende, *Cuatrecasas 19145* (A, F, US); **Narino:** Putamayo, Páramo el Tábano, *Garcia Barriga 4527* (COL, US): woods near Pasto, *Jameson 476* (G, BM-in part, GH).

24. **Eriosorus Biardii** (Fée) A. F. Tryon, comb. nov.

FIG. 36, MAP 18

Anogramma Biardii Fée, Crypt. Vasc. Brés. 1:241, t. 77, f. 1. 1869. TYPE: *Glaziou 3331*, Brazil, Serra dos Orgãos, Rio de Janeiro, June 1869, Herb. Cosson P! photo GH; isotypes: B!, C!, K!, P!, S!, US! The second collection at Paris has a printed label indicating that it is from the Herb. Glaziou, with the date 27 May 69, which evidently indicates that the work of Fée was published in or later than June 1869.

Gymnogramma extensa Bak. in Mart. Fl. Bras. 1(2):599. 1870. TYPE: *Glaziou 3331*, Brazil, Serra dos Orgãos, Rio de Janeiro, K!

Psilogramme Biardii (Fée) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 336. 1882.

Rhizome repent, compact with short internodes, 3–4 mm. in diameter, with rigid, appressed, ruddy to deep brown trichomes or bristles, at the base 1–4 cells wide, 1 or 2 cells thick, the apical cell elongate or globose. *Leaves* erect 45–90 cm. long. *Petiole* subterete near the rhizome, channeled at the apex, castaneous, less than 1/2 as long as the lamina, nearly glabrous, the base with few, short, erect brown trichomes with globose apical cell. *Lamina* elongate-rhomboid, the pinnae oriented in one plane, the central ones longer than those at the apex or base (the basal usually deteriorated), 4-pinnate, 28–69 cm. long, 7–19 cm. wide, determinate, the apical bud minute with sparse trichomes. *Rachis* straight, rarely slightly fractiflex, the upper surface strongly channeled, the lower convex, castaneous, the apex tan or green, usually glabrous. *Pinnae* slightly ascending, departing at an angle less than 90°, deltoid, elongate-triangular, the basiscopic side slightly larger, 3.5–9.0 cm. long, 2.5–4.5 cm. wide, herbaceous; *upper surface* sparsely pubescent to nearly glabrous, the trichomes clear, the apical cell usually elongate; *lower surface* with similar indument or with more trichomes

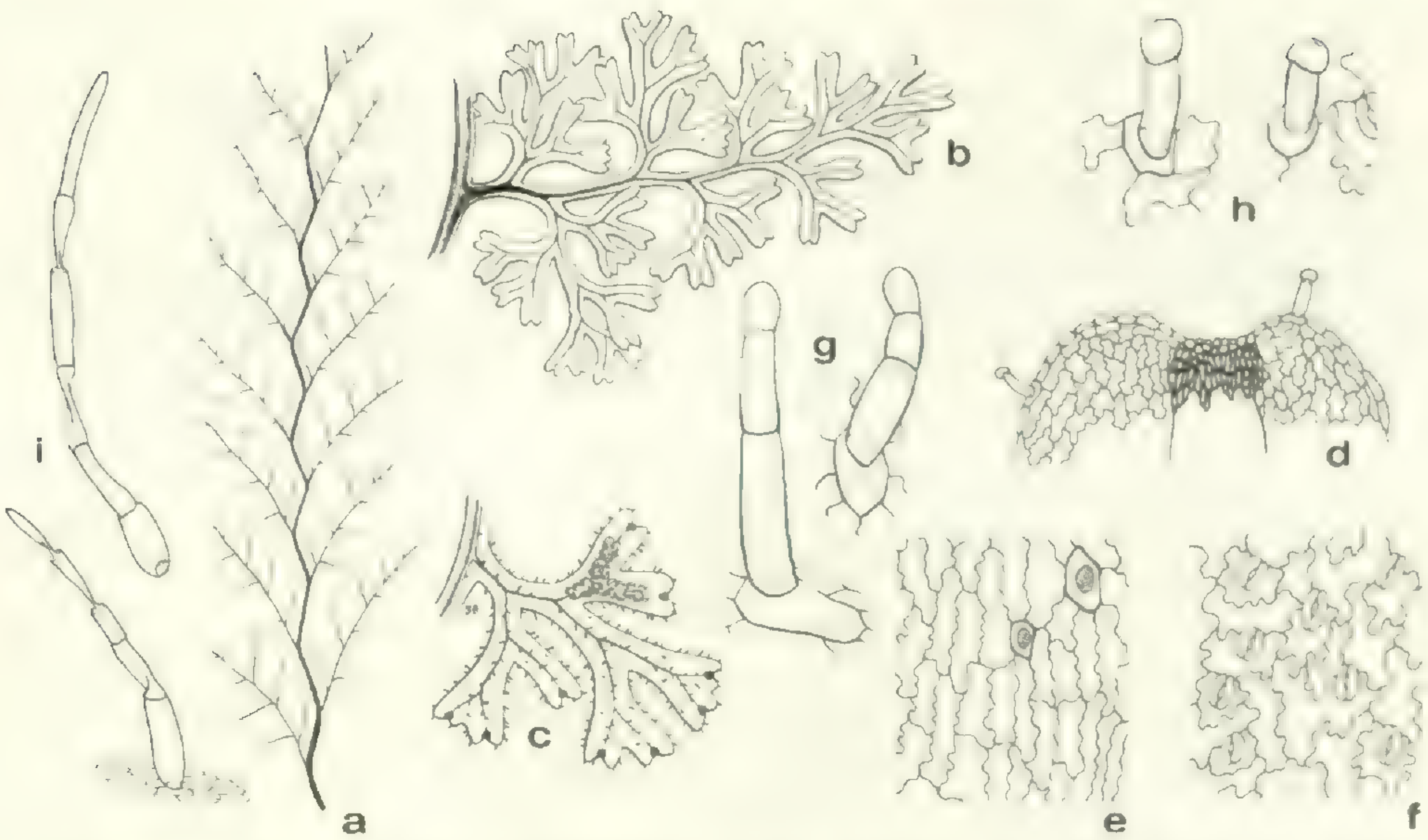


FIG. 35. *Eriosorus Ewanii:* a, diagram of pinna rachises and portion of the rachis, × 1/3, *Jameson,* Volcan Pasto (GH); b, pinnule with veins, × 1–2/3; c, tertiary segment with veins and glands, sporangia on one ultimate segment, × 2–2/3; d, margin on terminal portion of lobe with thickened vein end and glands, × 20; e, upper epidermis with basal cells of trichome darker; f, lower epidermis; g, h, glandular trichomes from lamina; g, upper surface; h, lower surface, all × 40, from *Ewan 16316* (GH); i, rhizome trichomes of young plant, lower with elongate cells of rhizome at base, × 20, *Cuatrecasas 19145* (A).

among the sporangia, the apical cell elongate; *stalk* 2–4 mm. long, sulcate on the upper surface, with ridges continuous with those on the rachis, glabrous; *pinnules* elongate-ovate or -triangular; *ultimate segments* usually cuneate, with bifid lobes as long as or slightly shorter than broad, the margins retuse, usually incurved or plane; *veins* ending short of the margin, slightly enlarged (the terminal portion obscure on the abaxial surface); *border* narrow, clear, 1 or 2 rows of elongated cells, the marginal ones protruding at the apical end, those at the segment apex about as long as broad and slightly protruding. *Sporangia* most abundant on base of the ultimate and on the penultimate veins, the stalk short, of 1 or 2 tiers of clear cells, the annulus often irregular, of 16–20 indurated cells. *Spores* deep brown, the proximal face with dense tubercles usually coalescent in a broad ridge parallel to the triradiate scar, with a narrow equatorial flange, sometimes irregular, the angles not projecting, the distal face with a smooth, central areola.

The lamina tissue is herbaceous and not unusually thickened, but the vein ends are submerged on the abaxial surface. In the shape of the ultimate segments, segment borders, and in lamina indument the species is similar to *E. flexuosus.* It is readily distinguished by the smaller, linear leaves and predominantly straight, dark colored rachises. In the suite of specimens collected by Brade 19246, some leaves have slightly flexuose rachises and

FIG. 36. *Eriosorus Biardii:* a, habit with some pinnae in detail and rachises of others, × 1/3, *Brade 19246* (RB); b, pinnule with veins and some sporangia, × 1–1/3, *Glaziou 3111* (P); c, margin on terminal portion of lobe with vein end, × 20; d, e, epidermis × 40; d upper epidermis, e lower epidermis, all from *Glaziou 3111* (P); f, g, lamina trichomes, × 40, f from upper surface, g lower surface along vein, both *Brade 16515* (GH); h, rhizome bristles with small basal cells from rhizome epidermis, × 20, *Brade 19246* (RB).

the ultimate segments are strongly bifid. In these and other collections the width of the lamina is especially variable. The geographic associations are useful here because *E. Biardii* occurs in Espirito Santo and the only Brazilian record of *E. flexuosus* is from that state, made by Glaziou in 1884. On the basis of this geographical association and morphological similarities of these

species, *E. Biardii* is considered most closely related to *E. flexuosus*. In partial shade, between shrubs. Brazil, at 2000 and 2100 m.

ADDITIONAL SPECIMENS EXAMINED: **Brazil. Espírito Santo:** Castelo, *Brade 19246* (RB). **Rio de Janeiro:** Pedra-Assú, *Brade 9523* (R), Serra dos Orgãos, Campo dos Antas, *16515* (BM, GH, RB, S, US); Therezopolis, *Glaziou 78* in April 1868 (R).

25. **Eriosorus glaberrimus** (Maxon) Scamman, Contrib. Gray Herb. 191:85. 1962

FIG. 37, MAP 21

Psilogramme glaberrima Maxon, Bull. Torrey Club 42:82. 1915. TYPE: *Tonduz 12531*, Costa Rica, La Palma, September 4, 1898, US!; isotype: P!; paratypes: from the same place, *Brade*, March 17, 1908, US! P!, S!, S-PA!; *Maxon 498* US.

Gymnogramma glaberrima (Maxon) C. Chr. Ind. Fil. Suppl. Prélim. 19. 1917.

Rhizome repent with short internodes, ca. 3–8 mm. in diameter, the trichomes or bristles, crispate or rigid, ruddy to deep brown, at the base 1–7 cells wide, 1–3 cells thick, the apical cell globose. *Leaves* scandent or subscandent, erect in young plants, up to 3.6 m. long. *Petiole* subterete or plane on the upper surface, lustrous, castaneous throughout, ca. 1/5 or 1/4 as long as the lamina, sparsely pubescent, the trichomes rigid, tan or light brown with a globose, glandular apical cell. *Lamina* elongate, with the pinnae oriented in one plane, the central ones somewhat longer than those at the apex or base, usually 5-pinnate, the smallest fertile specimens 21 cm. long and 10 cm. wide, the longest complete specimens 300 cm. long and 50 cm. wide, indeterminate, the apical bud usually minute, glabrous or trichomes rare. *Rachis* fractiflex, the upper surface strongly channeled, lustrous castaneous throughout, glabrous or with sparse trichomes mostly at the pinnae axils, the trichomes light brown or tan, the apical cell globose. *Pinnae* descending from the rachis, departing in an arc or broad angle greater than 90° (the pinnae rachises fractiflex, the pinnule stalks strongly curved, forming arcs ascending toward the pinna apex), deltoid or elongate-triangular, the basiscopic side slightly larger, 8–31 cm. long, 4–20 cm. wide, herbaceous or somewhat papyraceous; *upper surface* usually glabrous, the young leaves with a few clear or tan trichomes, the apical cell elongate; *lower surface* glabrous or with few trichomes among the sporangia, similar to those above; *stalk* 1–4 cm. long, sulcate on the upper surface, the ridges continuous with those of the rachis, glabrous; *pinnules* elongate-triangular or ovate; *ultimate segments* usually bifid, cuneate, with slender lobes about as long as broad or shorter (the sinus usually wide), the margins retuse or more deeply cleft, plane; *veins* extending to the margin usually terminating in a cleft, not or slightly enlarged; *border* narrow, clear, 1–3 rows of elongated cells, those along the edge usually bulging at the apical end, those at the apex about as broad as long. *Sporangia* along the ultimate and penultimate veins, the stalk short, of 1 or 2 tiers of clear cells, the annulus of 17–26 indurated cells. *Spores* deep brown, the proximal face with prominently sculptured bands parallel to the triradiate scar, the equatorial flange moder-

ately broad, the angles not projecting, the distal face with a few coarse tubercles within the central areola, or smooth.

The scandent leaf form of *Eriosorus glaberrimus* somewhat resembles that of *E. flexuosus* although there are basic differences in the orientation of the rachises, in the form of the leaf apex and disposition of the pinnules. The plants occur in wet forest and are ecologically more restricted than *E. flexuosus*. Meiotic cells of plants from La Hondura have 87 bivalents at diakinesis. This is regarded as another hexaploid similar to other Costa Rican species. It is the only species, among six in Central America, without marked affinities with species in the Andean region. On the basis of the characters noted above, distinguishing it from *E. flexuosus*, as well as the ultimate segments with broader, spreading lobes, and the dark spores, it seems more likely to have originated from an element formerly more widely distributed than from species now in Costa Rica.

Scandent or subscandent in wet forests or on moist road banks in the lower montane zone. Nicaragua and Costa Rica, at 1230–2300 m.

ADDITIONAL SPECIMENS EXAMINED: **Nicaragua.** Omotepec, *C. Wright* (GH, K, US). **Costa Rica.** Cob Blanco, *Wercklé 16438*, May 1901 (P, S-PA). **Heredia:** Vara Blanca, *Haupt 205* (US); slope of Volcán Barba, *Scamman & Holdridge 7929* (GH). **Alajuela:** Cerros de la Balsa de San Ramon, *Brenes 4970* (F, P). **San José:** La Palma 17.3. 1908, *Brade 84* (B, P, S-PA); *Maxon & Harvey 7940* (S-PA, US); at 1510 m., *Tryon & Tryon 7061, 7064, 7065, 7066, 7067, 7068* (GH); Cola de Gallo, *Stork 1952* (US). **Cartago:** Santa Clara de Cartago, *Lankester*, 1930 (US); La Estrella, *Standley 39424* (US); between El Empalme & La Sierra, *Tryon & Tryon 7058* (GH); above San Isidro, *Weber 6014* (GH); near La Sierra, *L. O. Williams* et al. *28046* (F).

PUTATIVE HYBRIDS INVOLVING ERIOSORUS GLABERRIMUS

Eriosorus glaberrimus × Eriosorus congestus

La Palma, the locality of the type specimen of *E. glaberrimus*, is now largely cleared and the land is used for grazing. However, there are still a few scattered trees and patches of woodland, especially some distance from the main roadway leading to La Hondura. We found several plants of *E. glaberrimus* there with scandent leaves nearly four meters long. In open areas, on and about the bases of old tree stumps, *E. congestus* was abundant. The intermediate plant, growing with *E. glaberrimus*, was scandent with elongate leaves. The rachises are slightly flexuose, not at all arcuate and have large pinnules and broad, cuneate ultimate segments similar to those of *E. congestus*. Unfortunately, the sporangia were too mature for cytological fixation, and the spores were aborted. **Costa Rica. San José:** La Palma, on road to La Hondura, 1510 m., *Tryon & Tryon 7062* (GH).

FIG. 37. *Eriosorus glaberrimus:* a, habit with three pinnae in detail and rachises of others, a portion of the main rachis omitted, × 1/3; b, apical bud, enlarged; c, tertiary segment with veins and some sporangia, × 1, all from *Tryon & Tryon 7061* (GH); d, two ultimate segments with veins, and sporangia on one, × 2–2/3; e, f, margins on terminal portion of lobes with vein ends, × 34; d,e, *Brade 84* (S-PA); f, *Tryon & Tryon 7061* (GH); g, h, epidermis; g upper epidermis, h lower epidermis; i, trichome from sorus, all × 40, *Brade 84* (S-PA); j, rhizome bristles, elongate cells of rhizome, at base, × 20, *Tryon & Tryon 7058* (GH).

DUBIOUS AND EXCLUDED NAMES

Eriosorus Lechleri (Kuhn) A. F. Tryon, Rhodora **65**:56. 1963. TYPE: *Lechler 2262*, Peru, Puno, San Gavan, B! photo GH. (*Gymnogramma Lechleri* Mett. ex Kuhn, Linnaea **36**:71. 1869, *Psilogramme Lechleri* (Kuhn) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 339. 1882). A further study of

Andean *Eriosorus* results in the conclusion that the single, incomplete leaf collected by Lechler cannot be identified with any known species.

Eriosorus Ruizianus Fée, Gen. Fil. 152, t. 13, f. 2. 1852=*Pityrogramma ferruginea* (Kze.) Maxon.

Gymnogramma domingensis Bak. Ann. Bot. **5**:485. 1891. TYPE: Hort. Bull. S29, 1875, Santo Domingo, Alto Carusal, 7000 ft. K! photos GH, US and fragment. It is quite possible that the three incomplete leaves which represent this name may be from a cultivated plant because the petioles are abnormally thickened. William Bull was a horticulturalist growing orchids primarily, in Chelsea.

Gymnogramma glandulifera Hieron. Hedwigia **48**:217. 1901. TYPE: *Stübel* 299, Colombia, inter Rejoy et Santiago, B! photo GH. The vein ends terminate short of the margin and suggest the specimen may be a variant form of *E. hispidulus*, but I cannot place it there with confidence.

Gymnogramma hirsutula Mett. var. *glandulosa* Hieron. Hedwigia **48**:220. 1909. TYPE: *Stübel 187*, Colombia, Río Paes, B! photo GH. This collection appears to represent a hybrid between *Jamesonia* and possibly one of the linear leaved species of *Eriosorus* but I cannot confidently identify the material as a species of either genus.

Gymnogramma Kunzei Ettinghausen, Frankräuter der Jetztwelt 56, t. 31, f. 5 Wien. 1865, nom. nud. The figure is wholly inadequate to meet the requirements of Article 44 of the Code of Nomenclature.

Gymnogramma laserpitiifolia Kze. Bot. Zeit. 3:285. 1845. TYPE: *Moritz* 39 & 79 (sterile) Venezuela, Caracas. The Moritz collections have not been seen but the description specifying flexuous rachises suggests that they may represent *E. flexuosus*.

Gymnogramma Mathewsii Hook. var. *glabriuscula* Hieron. Engl. Bot. Jahrb. **34**:480. 1904. TYPE: *Lehmann* 3238, Colombia, Cauca, Ritaraldo, B! isotype G! photo GH. The label notes that the specimens were epiphytes growing in a shaded situation which may account for the unusually thin leaf texture and slightly elongated internodes. The dark costa and compact form of the pinnae with bicolorous trichomes seem to relate the specimens to *E. rufescens*.

Gymnogramma Regnelliana (Mett. ex Bak.) Christ, Pl. Nov. Mineiras **2**:18. 1900. Based on *Cheilanthes Regnelliana* Mett. ex Baker, Fl. Bras. **2**:391, t. 43, f. 1. 1870, which is *Cheilanthes*. Christ cited *Schwacke 12745* which is *E. Sellowianus*, but the combination he made is excluded from *Eriosorus*.

Gymnogramma subscandens Sodiro, Crypt. Vas. Quitensis, 401. 1893. TYPE: *Sodiro*, Ecuador, Volcán Corazón. On the basis of such characters as quadripinnatifid fronds, a flexuose rachis and linear ultimate segments, noted in the description, the name may represent *E. flexuosus* var. *flexuosus*.

Gymnogramma tortuosa Sodiro, op. cit. 401. 1893. TYPE: *Sodiro*, Ecuador, Volcán Corazón. A fragment of a Sodiro collection with these data at P does not represent *E. flexuosus* but is too incomplete for identification.

LITERATURE CITED

ATKINSON, L. R. 1960. The Schizaeaceae: The gametophyte of *Mohria*. Phytomorphology **10**:351–367.

————————. 1962. The Schizaeaceae: The gametophyte of *Anemia*. Phytomorphology **12**:264–288.

BOWER, F. O. 1928. The Ferns. Vol. 3. The Leptosporangiate Ferns. University Press, Cambridge, England.

CHRISTENSEN, C. 1938. Filicinae, in Manual of Pteridology. Martinus Nijhoff. The Hague.

COPELAND, E. B. 1947. Genera Filicum. Chronica Botanica. Waltham, Massachusetts.
DESVAUX, N. A. 1827. Prodrome de la famille des fougères. Mém. Soc. Linn. Paris 6:171–337.
DUNZINGER, G. A. 1901. Beiträge zur Kenntnis der Morphologie und Anatomie der Genera *Hemionitis*, *Gymnogramme* und *Jamesonia*. Dissert. Univ. Münch. München.
ERDTMAN, G. 1957. Pollen and Spore Morphology. Plant Taxonomy. Almqvist & Wiksells. Stockholm.
ESAU, K. 1953. Plant Anatomy. John Wiley & Sons, Inc. New York.
FÉE, M. A. 1852. Exposition des Genres de la Famille des Polypodiacées (Mem. Fam. Foug. 5) Paris & Strasbourg.
HAFSTEN, U. 1960. Pleistocene development of vegetation and climate in Tristan da Cunha and Gough island. Univ. Bergen Årb. Naturv. **20**:1–45.
VAN DER HAMMEN, T. & E. GONZALES. 1960. Upper pleistocene and holocene climate and vegetation of the "Sabana de Bogota" Colombia, South America. Leidse Geol. Meded. **25**:261–315.
HOOKER, W. J. & R. K. GREVILLE. 1827–1831. Icones Filicum. London.
HOOKER, W. J. & J. G. BAKER. 1865–1868. Synopsis Filicum, London. Ed. 2. 1874. London.
KARSTEN, H. G. 1859–1869. Florae Columbiae. Berlin.
KONDO, T. 1962. A Contribution to the Study of the Fern Stomata. Bull. Shizuoka Univ. Faculty Ed. **13**:239–267.
KUHN, M. 1868–1869. Reliquiae Mettenianae. Linnaea **35**:385–394; **36**:41–149.
————————. 1882. Die Gruppe der Chaetopterides unter den Polypodiaceen. Fests. 50 Jub. Reals. Berl. (Chaetop.) 323–384.
KUNZE, G. 1846. Farrnkräuter. Leipzig.
LANJOUW, J. & F. A. STAFLEU. 1964. Index Herbariorum. Reg. Veget. 31:1–251.
LELLINGER, D. B. 1967. *Pterozonium*, in Maguire, The Botany of the Guayana Highland–Part 7. **17**:1–23.
MANTON, I. 1950. Problems of Cytology and Evolution in the Pteridophyta. Cambridge, England.
MANTON, I. & G. VIDA. 1968. Cytology of the Fern Flora of Tristan da Cunha. Proc. Roy. Soc. B **170**:361–379.
MAXON, W. R. 1915. The North American Species of *Psilogramme*. Bull. Torrey Bot. Club **42**:79–86.
METCALFE, C. R. 1960. Anatomy of the Monocotyledons. 1. Gramineae. Oxford, Clarendon Press.
METTENIUS, G. 1864. Filices. In Triana & Planchon, Prod. Florae Novo-Granatensis Ann. Sci. Nat. V, **2**:193–271.
MICKEL, J. T. 1967. The Phylogenetic Position of *Anemia colimensis*. Amer. Jour. Bot. **54**:432–437.
MOMOSE, S. 1964. The Prothallium of *Ceratopteris*. Jour. Jap. Bot. 39:225–235.
OGURA, Y. 1938. Anatomie der Vegetationsorgane der Pteridophyten, in Linsbauer, Handbuch der Pflanzenanatomie 7(2). Berlin.
PETIT-THOUARS, L. M. A. DU. 1808. Esquisse de la flore de l'île de Tristan d'Acugna. Paris.
PICHI-SERMOLLI, R. E. G. 1966. Adumbratio florae Aethiopicae 13. Hemionitidaceae. Webbia **21**:487–505.
SCAMMAN, E. 1962. The Genus *Eriosorus* in Costa Rica. Contrib. Gray Herb. **191**:81–89.

Swartz, Olof. 1806. Synopsis Filicum. Kiliae.
Tryon, A. F. 1962. A Monograph of the Fern Genus *Jamesonia*. Contrib. Gray Herb. **191**:109–197.
———. 1963. Notes on the Fern Genus *Eriosorus*. Rhodora **65**:56–57.
———. 1965. Paraphyses in the Ferns. Taxon **14**:214–218.
———. 1966. Origin of the Fern Flora of Tristan da Cunha. Brit. Fern Gaz. **9**:269–276.
———. 1968. Evolutionary studies in a group of Costa Rican Ferns. Abstr. Amer. Journ. Bot. **55**:735–736.
Tryon, R. M. 1960. A glossary of some terms relating to the fern leaf. Taxon **9**:104–109.
———. 1962. Taxonomic fern notes 2, *Pityrogramma* (including *Trismeria*) and *Anogramma*. Contrib. Gray Herb. **189**:52–76.
———. 1964. The Ferns of Peru. Polypodiaceae. Contrib. Gray Herb. **194**:1–253.
Tschudy, R. H. & B. D. Tschudy. 1965. Modern Fern Spores of Rancho Grande, Venezuela. Acta Bot. Ven. **1**:9–72.
Walker, T. G. 1966. A Cytotaxonomic Survey of the Pteridophytes of Jamaica. Trans. Roy. Soc. Edinburgh **66**:169–237.
Underwood, L. M. 1902. American Ferns 4. The Genus Gymnogramme of the Synopsis Filicum. Bull. Torrey Bot. Club **26**:617–634.

A REVISION OF THE GENUS MENKEA

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There are approximately fifty endemic species of *Cruciferae* in Australia. Many were first described as species in genera otherwise extra-Australian. They have since had a varied nomenclatural history, being transferred from one genus to another, until O. E. Schulz (1924, 1933) described several new genera to accommodate them. Some, however, have always been placed in genera entirely Australian, one of which is *Menkea* Lehmann, now including six species of small winter- and spring-flowering ephemerals of central and southern Australia.

Most of the early Australian botanical collections were made by English and French explorers, but in 1838 a German collector, Johann Ludwig Preiss, went to Western Australia, returning three years later with extensive collections of plants and animals from the southwestern part of the then Swan River Colony. The plants, finally listed under 2718 numbers, were turned over to various European specialists for study with the results edited by J. G. C. Lehmann of Hamburg and published from 1844 to 1848 as Plantae Preissianae.

The treatment of the *Cruciferae* (Vol. 1:257–262) was prepared by Alexander von Bunge and published in December, 1844 or January, 1845, but Lehmann, who was director of the botanic garden at Hamburg, grew some plants from seed brought back by Preiss and published a description of a new genus, *Menkea*, and one species, *M. australis*, in the Index Seminum of the garden for 1843. Lehmann offered no suggestions concerning the affinities of the genus except to remark "nov. genus Cruciferarum e Commelinearum tribu," a slip corrected by Bunge in his treatment to "e Camelinearum tribu." Their concept of the *Camelineae* was probably that of de Candolle and included genera in which the siliques are completely dehiscent and not compressed contrary to the septum, and the embryos notorrhizal. Bunge remarked that *Menkea* is a very clearly defined genus, "affine ex characteribus Orobio et Eudemati, ex habitu Stenopetalo. . ." and went on to point out that it differed from the first two genera by the "quadriseriate" seeds and the habit, and from *Stenopetalum* by the unilocular siliques and petals that are not elongated. *Orobium* Reichenb., now generally included in *Aphragmus*, and *Eudema* resemble *Menkea* only superficially in that the siliques may be eseptate.

The first two species described in *Menkea, M. australis* and *M. draboides* (Hook.) Benth., have small oblong or obovate siliques which are strongly compressed in the plane of the replum so that the valves are nearly flat; the septum is much reduced or absent and the ovules are biseriate and very numerous. *Menkea draboides* was described in 1844 as a species of *Stenopetalum* by Hooker, who apparently did not then know of Lehmann's publication of *Menkea*. He stated that in spite of the eseptate siliques he was reluctant to separate the species from *Stenopetalum,* that is, from S. *lineare* R. Br. ex DC., which is, however, very different in habit and has nearly cylindric, few-seeded siliques and greatly elongated petals, and from his own *Stenopetalum procumbens* which is *Menkea australis*. In 1874 Mueller described *M. sphaerocarpa* and remarked, "Speciem . . . a genere removere nolui propter valvas fructuum turgentes, quia enim Cochlearia species siliculis tum planis tum turgidissimis includerit"; since then it has been accepted that *Menkea* includes plants both with compressed and inflated siliques. The genus, as now delimited, consists of a group of species characterized by small compressed or inflated siliques in which the septum is reduced to a very narrow rim or completely gone and the ovules are biseriate and numerous.

Schulz (1936) placed *Menkea,* including only *M. australis, M. draboides* and *M. sphaerocarpa,* in subtribe *Brayineae* of the *Sisymbrieae* which is distinguished from subtribe *Camelinineae* [*sensu* Schulz] by the leaves being not amplexicaul and the seeds not mucose. He put *Stenopetalum* into the monogeneric tribe *Stenopetaleae* which essentially differs from the *Sisymbrieae* only by the erect calyx and elongated petals. I am reluctant to offer any opinions about the relationships of *Menkea* to extra-Australian genera, but I think that among the endemic genera, *Menkea* is perhaps closer to *Stenopetalum* than to any of those in the *Arabidopsidineae* (Shaw, 1965) or to those which have obcompressed siliques. Although Schulz, in 1933, transferred *M. villosula* to his newly described genus *Phlegmatospermum,* this was a result of his having relied on the original description of the species which contains some inaccuracies, and the two genera are, I think, not closely related; the three or four species of *Phlegmatospermum* all have strongly obcompressed, few-seeded siliques and are pubescent with malpighiaceous trichomes.

All six species of *Menkea* are ephemerals of arid and semi-arid parts of central and southern Australia. Often they are found in

places such as creek beds and clay pans or in any shallow depression which might receive runoff water. There are various notes on herbarium labels indicating that the plants were growing on soils derived from limestone and calciphily is not uncommon in the family. The center of distribution would seem to be in northern South Australia where five species have been found. The known range of each species is shown by the maps and the cited specimens; in each case the species may be more widely spread, but the plants are short-lived and, in part, grow in an area which is not well-known botanically.

The genus is named for C. T. Menke (1791–1861), a physician and amateur malacologist of Bad Pyrmont.

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SYSTEMATIC TREATMENT

Menkea Lehmann, Ind. Sem. Hort. Hamburg. 8. 1843

TYPE SPECIES: *Menkea australis* Lehmann, Ind. Sem. Hort. Hamburg. 8. 1843.

Plants small glabrous or villous annuals; stems several, prostrate or erect from a rosette of basal leaves; basal leaves linear to oblanceolate, the blades entire, dentate or pinnatisect and narrowing to a slender petiole; cauline leaves few and remote, obovate or spathulate, entire or coarsely dentate; inflorescences ebracteate, buds subglobose or ovoid; sepals spreading and sometimes persistent, sometimes saccate or cucullate; petals white, yellow, or pink to mauve, as long as to twice as long as the sepals, oblong to obovate or clearly differentiated into blade and claw, the claw often rather broad; stamens erect or spreading; glandular tissue semi-circular to square or several-angled around the single stamens and subtending the paired stamens; ovules 10–130 per ovary; siliques completely dehiscent, unilocular by more or less complete reduction of the septum, subglobose to obovoid or ellipsoid, or strongly compressed and elliptic or oblong; styles very short or obsolete; stigmas depressed-capitate, slightly expanded; seeds biseriate and numerous, oblong or ellipsoid to ovoid; embryo notorrhizal.

KEY TO THE SPECIES OF MENKEA

A. Plants usually prostrate and spreading; siliques strongly compressed, the valves nearly flat.
  B. Ovaries and siliques glabrous.
    C. Petals usually white; septum completely reduced; ovules 40–80 per ovary ..... 1. *M. australis.*
    C. Petals bright yellow; septum present as a narrow rim; ovules 10–40 per ovary ..... 2. *M. lutea.*
  B. Ovaries and siliques papillose and often twisted. .... 3. *M. draboides.*
A. Plants often erect; siliques subterete in section, the valves concave.
  D. Plants villous with simple trichomes ..... 4. *M. villosula.*
  D. Plants completely glabrous.
    E. Petals white or cream-colored, 2–3.7 mm. long; leaves subsucculent and entire ..... 5. *M. crassa.*
    E. Petals usually mauve or pink, 3–5.2 mm. long; basal leaves not conspicuously succulent, usually lobed or dentate .... 6. *M. sphaerocarpa.*

1. **Menkea australis** Lehm., Ind. Sem. Hort. Hamburg. 8. 1843

MAP 1

HOLOTYPE: Western Australia: without exact locality; *Preiss 1937* (LU); probable isotype (MEL 7669).

Stenopetalum procumbens Hook., Icon. Pl. t. 610. 1844. HOLOTYPE: Western Australia: Swan River; *Drummond 3* (K).

Menkea procumbens (Hook.) F. Muell., Fragm. **2**:142. 1861.

Menkea coolgardiensis Sp. Moore, Journ. Bot. **35**:162. 1897. HOLOTYPE: Western Australia: near Coolgardie; *Spencer Moore,* 1895 (BM); photo (AD).

Plant a glabrous prostrate annual; stems 5–15 (-25) cm. long, several, usually branched, frequently showing red-purple or red-brown pigmentation; basal leaves to 5 cm. long and 4 mm. wide, spathulate, entire to pinnatisect with several lobes per side and narrowing to a short petiole, marcescent; cauline leaves to 2 cm. long and 7 mm. wide (usually ca. 1 cm. × 4 mm.), narrowly obovate to elliptic, entire or shallowly lobed, sessile or shortly petiolate; inflorescences initially lax and soon elongating, the pedicels often 1 cm. distant, buds subglobose to ovoid; sepals 1–2 (2.5) mm. long, 0.5–1.2 mm. wide, oblong to elliptic or (ob-)ovate, sometimes cucullate, green to pink or lavender; petals 1.3–2.5 mm. long, 0.4–0.9 mm. wide, white or pink to mauve, rather coarsely veined, cuneate or obovate or oblong, usually subacute, the margins entire or sinuate; stamens 1.2–2.2 mm. long, the filaments slender and little expanded; lateral glands square around the single stamens and subtending the paired stamens, but absent between the latter; ovules ca. 20–40 per locule; infructescences loose, the pedicels to 15 mm. long and usually divaricate, but sometimes horizontal or recurved; siliques 3.5–7 mm. long, 1.5–3.5 mm. wide, elliptic or ± obovate and markedly compressed, sessile; styles very short or absent, the stigmas small and depressed-capitate; septum obsolete; seeds ca. 0.3–0.4 mm. long, oblong or square or sometimes ellipsoid, orange-brown to dark red-brown; cotyledons as long as or slightly longer than the radicle.

REPRESENTATIVE SPECIMENS: **South Australia.** Evelyn Downs, *Ising,* 1952 (AD); Mt. Lynhurst, *Koch* 326 (AD, BM, K, NSW 77564); Warren's Gorge,

near Quorn, *anon.*, 1916 (AD); Koonamore, *Osborn,* 1928 (SYD); Wynarka, *Ising,* 1960 (AD); Whyalla-Kimba, *Higginson,* 1955 (AD); Ooldea, *Cleland,* 1935 (AD); Maralinga, *Hill 749* (BM). **New South Wales.** Nyngan, *Boorman,* 1903 (GH, NSW 77559); Cobar, *Abrahams,* 1911 (NSW 77560); Broken Hill, *Morris* 393 (NSW 77563); "Zara," Wanganella via Hay, *Officer,* 1917 (AD); Murray and Darling River, *Mueller & Beckler* s.n. (MEL 7665, MELU). **Victoria.** Swan Hill, *McAdams 89* (MEL 11005); Hattah, *Carr,* 1955 (MELU); northwest of Lake Albacutya, *French,* 1887 (MEL 7664); Nhill, *St. Eloy D'Alton 4* (MEL 7663). **Western Australia.** 4 miles south of Sandstone, *George 5663* (PERTH); near Laverton, *George 3743* (PERTH); Northam, *Fitzgerald,* 1898 (NSW 77565); Swan River, *Drummond 2nd series no. 48* (BM, K, LU, P, W).

This species is probably more widely spread than the cited collections indicate, and might be looked for in the southern part of the Northern Territory and in southwestern Queensland. Although not uncommon, the plants are prostrate and short-lived and are easily overlooked by collectors. In habit, *Menkea australis* somewhat resembles *Hymenolobus procumbens* (L.) Nutt. ex Schinz & Thell., but the latter is distinguished by the siliques which are completely septate.

In the protologue, Lehmann neither cited specimens nor mentioned a locality but remarked "Semina in Australia occidentali ex herbario Preissiano accepimus.", indicating that the descriptions are based on material collected in Western Australia by Ludwig Preiss during his stay there in 1838–1841. Bunge, who prepared the treatment of the *Cruciferae* for Plantae Preissianae, cited *Preiss 1937* under *Menkea australis,* so it is likely that the material under that number in Lehmann's own herbarium is the holotype. On Lehmann's death in 1860, the Preiss collections in his herbarium were purchased by Agardh (Bot. Zeit. **20**:255. 1862) and are still housed at Lund.

Menkea coolgardiensis is known only from Spencer Moore's original collection. Mr. A. S. George, Australian Liaison Officer during 1968, kindly examined this specimen at the British Museum (Natural History) and reported that, in his opinion, it is *M. australis.* Moore described his material as "sparsim puberula" and remarked that this species differed from *M. australis* "chiefly in the much larger flowers with their persistent reflexed sepals, as well as in the differently shaped silicules." However, Mr. George found the plants to be quite glabrous; the size of the floral organs falls well within the range of those of *M. australis;* and the descriptions "siliculis oblongis compressis" and "Siliculae basi

breviter angustatae, 0.4 cm. long., vix 0.2 cm. lat." apply perfectly well to the siliques of *M. australis*.

For several years Mueller confused *Stenopetalum procumbens* Hook. (Icon. Pl. t. 610. 1844) with S. *draboides* Hook. (Icon. Pl. t. 617. 1844), both names based on collections made in the Swan River Colony by James Drummond. Hooker apparently did not know of the descriptions of *Menkea* and *M. australis* published by Lehmann, and published S. *procumbens* before the second fascicle (pp. 161–320) of the first volume of Plantae Preissianae (in which Bunge gave amplified descriptions) appeared in December, 1844 or January, 1845 (Stearn, Jour. Soc. Bibl. Nat. Hist. 1:203–205. 1939).

In 1862, Mueller made the combination *Menkea procumbens*, based on *Stenopetalum procumbens* Hook.; on the same page he gave a brief description of *M. australis*, correctly citing Lehmann's original description and the fuller one provided by Bunge, but he cited as a synonym S. *draboides* Hook., and remarked "Hujus speciei diagnosin juxta tabulam supra citatam [Icon. Pl. t. 617] exstruxi, quum plantam ipsam nondum viderim." Having seen no authentic material of S. *draboides*, Mueller assumed it to be the same as Lehmann's *M. australis*. It is surprising that he did not realize that Hooker's diagnosis and description of S. *procumbens* agree much better with the description given by Lehmann and Bunge of *M. australis* than do those of S. *draboides*. In particular, Hooker said of S. *draboides*, ". . . siliculis oblongo-obovatis compresso-planis subtortuosis unilocularibus (dissepimento nullo) minutissime puberuli-granulatis. . . ." The siliques of *M. australis* are never twisted and completely lack trichomes or papillae, while those of *M. draboides* are usually twisted and are always papillose. The taxonomy of these two species was clarified by Bentham (1863).

The German-Australian collector, Max Koch, whose collections were widely distributed to Australian, European and American herbaria, in listing the plants he had found at Mt. Lyndhurst in the Flinders Ranges of South Australia (Trans. Roy. Soc. S. Austral. **22**:102. 1898), said of *Menkea australis*, "My No. 326 is a variety differing from the typical form by the paucity of foliage. It is quite prostrate, racemes are filiform, flowers white, more minute than with *M. australis*, and the fruits somewhat narrower at the apex, and slightly wrinkled." Koch here confused *M. australis* with a hitherto undescribed species. On one sheet of

Koch 326 (AD) he noted "prostrate var: very different from typical form 270." However, the prostrate form *(Koch* 326) is true *M. australis* while *Koch 270,* also distributed as that species, is *M. crassa* E. Shaw, a species seldom found outside the Lake Eyre basin and the northern Flinders Ranges in South Australia.

2. **Menkea lutea** E. Shaw, sp. nov.

Map 1

Herba annua glabra caulibus gracilibus plerumque prostratis; folia basalia rosulata, spatulata vel obovata, plerumque pinnatisecta lobis 2–4 utroque latere, in petiolum longiorem angustata; folia caulina remota, ± obovata dentibus grossis 1–3 utroque latere, in petiolum angustum contracta, raro folia sessilia; racemi conferti plerumque floribus 20–40; sepala caduca, mediana quam lateralia parum maiora; petala lutea, plerumque anguste obovata sine ungue distincto autem nonnumquam lamina obovata, elliptica vel rhombea in unguem ± aequilongum vel breviorem attenuata; ovulae 5–20 in loculo; siliquae obovatae vel ellipticae valde latiseptales; semina ± ellipsoidea.

HOLOTYPE: Western Australia: Wingelena airstrip, Tomkinson Range (± 128° 48′ E., 26° 3′ S.), *Symon 2165* (AD); isotype (ADW).

Plant an erect or prostrate glabrous annual; stems to 4 dm. long, slender and flexuous and usually branched, often with some purple pigmentation, basal leaves to 6 cm. long and 10 mm. wide, spathulate to obovate, usually pinnatisect with 2–4 segments on a side, narrowing into a slender petiole nearly as long as the blade, often with much purple pigmentation; cauline leaves few, to 3 cm. long and 8 mm. wide, ± obovate with 1–3 coarse teeth per side, narrowing to a short petiole or sessile; inflorescences initially dense but rapidly elongating after anthesis, buds subglobose; sepals 1.7–2.3 mm. long, elliptic or oblong to ovate, sometimes cucullate; petals 1.8–2.8 mm. long, 0.8–1.2 mm. wide, bright yellow and coarsely veined, oblong to elongatedly obovate or sometimes with a distinct obovate or rhombic blade narrowing to a claw about as long; stamens 1.8–2.7 mm. long, filaments linear and slightly expanded at the base; glandular tissue square or pentagonal around the single stamens and subtending the paired stamens but not developed between these; ovules 5–20 per locule; infructescences loose, to 20 cm. long; pedicels 5–9 mm. long, divaricately spreading or erect; siliques 4–6.8 mm. long, 1.9–2.7 mm. wide, obovate to elliptic and much compressed, sessile or substipitate; styles 0.3–0.5 mm. long, stigmas small and depressed-capitate; septum reduced to a narrow rim, this present sometimes only at the proximal end of the silique; seeds 0.7–0.9 mm. long, oblong to ellipsoid, orange to yellow-brown cotyledons slightly shorter than the radicle.

SPECIMENS SEEN: **Western Australia.** Wingellina near Mt. Hinchley, *Cleland,* 1960 (AD); Blackstone Range Mining Camp, *George 4820* (PERTH). **South Australia.** Mt. Davies, *Cleland,* 1960 (AD); 10 miles northwest of Mt. Davies airstrip by road to Giles, *Wilson 2466* (AD). **Western Australia** or **South Australia.** Tompkinson Range, *Cleland,* 1954 (AD).

The Tomkinson and Blackstone Ranges were crossed on horseback by Ernest Giles in 1873. Richard Helms, botanical collector with the Elder Exploring Expedition (which relied on camels for

transport), spent several days in the western part of the Blackstone Range in 1891, but it is only in recent years, with the development of the weather station at Giles and the construction of airstrips, that this very remote area has been at all accessible to field biologists.

Menkea sphaerocarpa and *M. villosula* have also been found in the ranges of northwestern South Australia, but both species differ from *M. lutea* in that the siliques are subglobose; furthermore, *M. sphaerocarpa* has much larger mauve or pink petals and *M. villosula* is hirsute.

3. **Menkea draboides** (Hook.) Benth., Fl. Austral. **1**:80. 1863

MAP 2

Stenopetalum draboides Hook., Icon. Pl. t. 617. 1844. HOLOTYPE: Western Australia. Swan River: *Drummond* ("Crucif. n. 3.") (K); possible isotype (NSW 77566).

Plant a glabrous prostrate annual; stems to 0.6 dm. long, generally branched, often with reddish or purplish pigmentation; basal leaves to 3 cm. long and about 10 mm. wide, the blade ± obovate, entire or remotely lobed or dentate, narrowing to the slender petiole often as long as the blade; cauline leaves few, to 1.5 cm. long and 5 mm. wide, obovate or oblanceolate (sometimes falcate) entire or shallowly and remotely dentate or lobed, sessile or (the lowermost) shortly petiolate; inflorescences dense and few-flowered, buds ellipsoid or obovoid; sepals 1.8–2.3 mm. long, oblong, usually persistent; petals 2.5–3.0 mm. long, 1.0–1.4 mm. wide, apparently white or cream-colored, obovate or with an obovate to oblong blade narrowed to a ± linear claw; stamens 2.0–2.5 mm. long, filaments expanded at the base; glandular tissue horseshoe-shaped around the single stamens and subtending the paired stamens but absent between these; ovules 30–40 per locule; infructescences loose and quite short, pedicels to about 4 mm. long, usually spreading divaricately but sometimes erect; siliques 8–10 mm. long, 2–3 mm. wide, oblong to obovate, much compressed and frequently twisted, the valves densely papillose; styles short, the stigmas small, depressed and capitate; septum reduced to a very narrow rim; seeds oblong to ovoid, dark red-brown, but none fully developed seen.

SPECIMENS SEEN: **Western Australia.** Swan River: *Drummond,* 1843 (K); Swan River: *Drummond 2nd series* #49 (BM, K, LU, MEL 7670, W); Watheroo: *Koch 1758* (AD, NSW 77567); Watheroo: *Staer,* 1905 (E); Yilgarn: *Sayer,* 1889 (MEL 7687).

This, the least known species of *Menkea,* differs from the others in the usually twisted, papillose siliques. The fact that it seems not to have been collected since 1905 suggests that its habitats may have been destroyed although it is possible that the plants merely have gone unnoticed by collectors. There is also some confusion

about the provenance of Koch's collection; the labels are clearly marked "Watheroo" and "1758" and the date given is August, 1905. However, in the library of the National Herbarium of Victoria there is an manuscript résumé, written by Koch, of his collecting activities up to 1925. According to this, his collections of 1905 (numbers 1293 to 1385) were made near the inner rabbit-proof fence, "50 miles east of Watheroo Rwy. St.," with the following note: "but a considerable number of plants labelled later on among the Wooroloo plants." The material from Wooroloo was collected from 1906 to 1908 and includes Koch's numbers 1386 to 1851; the collection in question might have come from either place.

4. **Menkea villosula** (F. Muell. & Tate) Black, Trans. Roy. Soc. S. Austral. 40:62. 1916

MAP 2

Capsella villosula F. Muell. & Tate, Trans. Roy. Soc. S. Austral. **16**:335. 1896. HOLOTYPE: South Australia. Upper Arkaringa [Creek]; *Helms,* May 20, 1891 (MEL 7688); isotypes (AD, K, NSW 77571).

Phlegmatospermum villosulum (F. Muell. & Tate) Schulz, Bot. Jb. **66**:93. 1933.

Menkea hispidula Black, Trans. Roy. Soc. S. Austral. **39**:830. 1915. HOLOTYPE: South Australia. 15 miles west of Indulkana Springs: *White,* August 12, 1914 (AD—mounted with an isotype of *Capsella villosula*); isotype (MEL 7686).

Plant an erect annual, covered with simple spreading trichomes; stems 0.5–1.5 (3) dm. long, decumbent and usually branched, apparently lacking reddish or purplish pigmentation; basal leaves 2–7 cm. long, 4–9 mm. wide, oblanceolate and tapered to the slender petiole, entire to sinuate or coarsely dentate; cauline leaves few, to 4 cm. long and 4 mm. wide, oblanceolate to spathulate, entire or shallowly dentate, sessile or shortly petiolate (the lower leaves); inflorescences dense and many-flowered, buds subglobose; sepals 1.7–2.6 mm. long, 0.8–1.6 mm. wide elliptic or obovate to oblong and cucullate, the lateral sepals often nearly horizontal and hooding the single stamens; petals 2.3–3.8 mm. long, 0.8–1.6 mm. wide, bright yellow and coarsely veined, the blade elliptic to rhombic narrowing to a linear claw or the petal oblong to obovate with no distinction between blade and claw; stamens 1.8–3.0 mm. long, filaments often expanded at the base; glandular tissue dark green and fleshy, square or pentagonal around the single stamens and subtending the paired stamens, but not developed between these; ovules 20–70 per locule; infructescences loose, to ca. 15 cm. long; pedicels 5–8 (12) mm. long, erect to divaricate, often the proximal half parallel to the axis and then spreading; siliques 3.0–5.5 mm. long, 2–3 mm. wide, subglobose or ellipsoid, sometimes slightly compressed, sessile or on a short stipe, villous; styles 0.5–0.8 mm. long, stigmas fleshy and depressed and

Map 1. M. Australis (dots); M. crassa (triangles); M. lutea (squares)
Map 2. M. villosula (dots); M. sphaerocarpa (triangles); M. draboides (squares)

capitate; septum reduced to a rim 0.1–0.2 mm. wide or obsolete; seeds 0.4–0.5 mm. long, subglobose or shortly oblong, brown to dark red- or orange-brown; cotyledons a little shorter than the radicle.

REPRESENTATIVE SPECIMENS: **Northern Territory.** 3.6 miles west of Curtin Springs Homestead, *Chippendale* (BRI, CANB, MEL 7685, NSW 77568, NT 2862); Docker River near Petermann Range, *George 4959* (PERTH). **Western Australia.** 2 miles northwest of Giles Weather Station, *George 4925* (PERTH); Gunbarrel Highway, 3 miles east of Mungilli claypan, *George 5433* (PERTH); 14 miles east of Meekatharra, *Aplin 2460(d)* (PERTH); Upper Gascoyne, *Hoey,* 1963 (PERTH); Terin rockhole, Laverton-Warburton road, *George 4700* (PERTH); 16 miles south of Wiluna on Sandstone road, *George 5624* (PERTH). **South Australia.** 22 miles south of De Rose Hill station, *Perry 5520* (CANB, NSW 77569, NT); 48 miles east of Mt. Davies, *Wilson 2357* (AD); Musgrave Ranges, western slope to summit of Mt. Morris, *Eichler 17353* (AD); Piltardi, in Mann Ranges, *Cleland,* 1954 (AD); 22 km. south of Mt. Willoughby Homestead, *Shaw 515* (AD); ca. 30 km. north of the turnoff to Mable Creek Homestead, *Eichler 17238* (AD).

As pointed out by J. M. Black (Trans. Roy. Soc. S. Austral. 61:245. 1937) the plants in Helms' collection, on which Mueller and Tate based the name *Capsella villosula,* lack mature siliques and this is the apparent cause of some surprising inaccuracies, such as "two or three seeds in each cell," in the protologue. Black himself examined the holotype and found 50–60 ovules in each ovary. But before Black had seen this material, he described *Menkea hispidula* from plants collected near Indulkana Springs, about 12 miles west of Granite Downs Homestead, by S. A. White. In the protologue Black remarked that Captain White's specimens agreed well, "apart from the number of seeds," with the description of *C. villosula;* but not having seen the plants on which the latter name is based, he proceeded to describe the species as new, only to find in the following year, after Professor Ewart of Melbourne compared the collections of Helms and of White, that *M. hispidula* and *C. villosula* were conspecific and best placed in *Menkea.*

As a result of having seen only these plants with immature fruit, Mueller and Tate described the siliques as ". . .ellipsoid-oval, . . . ; the valves boat-shaped; the replum in the narrow diameter"; this, and the statement that there are two or three seeds in each fruit led O. E. Schulz, who knew the species only from the description, to transfer *Menkea villosula* to *Phlegmatospermum,* described as having "Ovarium ovoideum, 4–14-ovulatum; . . . Silicula a lateribus compressa, ovoidea, . . . ; valvulae naviculiformes, carinatae, desilientes. Semina prorata magna, . . . , recte

vel suboblique pleurorrhiza, ..." *Menkea villosula* does resemble *Phlegmatospermum* in that it is the only species of *Menkea* in which the seeds are truly mucose, and the plants are pubescent, although with spreading simple trichomes rather than with appressed branched ones, as are all species of *Phlegmatospermum*. However, the siliques of this species are never strongly obcompressed with keeled valves, as are those of *Phlegmatospermum*, the septum is obsolete or much reduced, and the seeds are numerous and very small. The inclusion of this species in *Menkea* makes incorrect that part of Schulz's key to the genera of *Sisymbrieae-Brayinae* (Nat. Pflanzenfam. ed. 2, 17b:290. 1936) in which *Menkea* follows the lead "Pflanze völlig kahl."

Menkea villosula is distinguished by the erect habit, bright yellow petals and dense covering of simple trichomes; the flowers are sweetly scented, the odor described by Helms in his field notes as "like hawthorn, mixed with heliotrope." In Australia, the only other species of this family having similar trichomes is *Lepidium oxytrichum* Sprague; however, the plants are much larger than those of *M. villosula*, the petals are white and the siliques are septate, two-seeded and strongly obcompressed.

5. **Menkea crassa** E. Shaw, sp. nov.

MAP 1

Herba annua glabra caulibus prostratis vel decumbentibus. Folia subsucculenta integra; basalia rosulata linearia vel spatulata in petiolum gracilem sensim angustata vel (superiora praecipue) cuneatim sessilia. Racemi conferti pauciflori. Sepala caduca, mediana quam lateralia parum maiora. Petala alba vel eburnea (raro lutea), lamina orbiculari vel obovata vel elliptica in unguem linearem attenuata; interdum petala anguste obovata sine unguo distincto. Ovulae ca. 25–55 in loculo. Silicula ellipsoidea vel sphaerica vel (ob-)ovoidea, teres vel parum latiseptalis. Semina ± ellipsoidea.

HOLOTYPE: South Australia. Sand dune immediately in front (west) of Mungerani Homestead; *Lothian 310* (AD).

Plant a glabrous prostrate or decumbent annual; stems to 1.5 (-2.5) dm. long, stout and usually branched, apparently lacking reddish or purplish pigmentation; basal leaves about 3 cm. long and 5 mm. wide, the blades entire and linear to spathulate tapering to the slender petiole, glaucous and rather fleshy; cauline leaves 1–4 cm. long, 0.3–0.6 cm. wide, obovate to spathulate, entire or sinuate, sessile (the upper leaves) or shortly petiolate, glaucous and subsucculent; inflorescences initially dense, buds subglobose; sepals 1.5–2.5 mm. long, ovate to elliptic or oblong, often cucullate; petals 2.0–3.7 mm. long, 1.0–2.3 mm. wide, white or cream-colored (rarely, yellow), coarsely veined, obovate or with an orbicular to obovate blade narrowing to a distinct claw; stamens 1.5–2.5 mm. long, the filaments expanded at the

base; glandular tissue square to pentagonal around the single stamens and subtending the paired stamens with a deltoid lobe between the bases of each pair of the latter; ovules ca. 25–55 per locule; infructescences loose, to ca. 8 cm. long; pedicels about 15 (-25) mm. long and usually divaricate but occasionally horizontal or erect; siliques ca. 3.5–6.5 mm. long, 1.8–3.6 mm. wide, ellipsoid to (ob-)ovoid, sometimes slightly compressed, sessile; styles 0.4–0.8 mm. long, stigmas small and depressed and capitate; septum reduced to a rim 0.2–0.3 mm. wide, broadest at the proximal end of the silique; seeds 0.5–0.6 mm. long, oblong to ellipsoid, dark orange-brown to red-brown; cotyledons shorter than the radicle.

REPRESENTATIVE SPECIMENS: **South Australia.** Sand hills around Lake Wittakilla, 40 miles from N. S. W. border (near junction of Boolkaree and Yandama Creeks, south of Lake Callabonna), *Béchervaise,* 1950 (AD, MEL 7677); Frome River bed, ca. 1½ miles north of Marree, *Shaw 189* (AD); Muloorina Station, in wet beds of claypan between Muloorina Station and Lake Eyre, *Hill 202* (AD); Mt. Lyndhurst, *Koch 270* (AD, B, BRI, K, MEL 7681, NSW 77553, 77554, 77555, P, W); north of Bopeechee, *Lothian 1301* (AD); Gidjee flood plain, 4 miles north of Oodnadatta, *Lothian 2053* (AD); Arkaringa Creek, *Helms,* 1891 (AD, MEL 7676, NSW 77557); between Musgrave Ranges and Birksgate Range, *Helms,* 1891 (AD); near lake Hart, *Whibley 1258* (AD). **Queensland.** Mulligan River, *Clarke,* 1904 (NSW 77551).

The specimens cited indicate the range of *Menkea crassa* as presently known, most of the forty collections seen having come from the Lake Eyre basin and the northern part of the Flinders Ranges. However, it is likely that more material will be obtained from the Lake Torrens basin as is suggested by *Whibley 1258* (AD) and a collection from Yudnapinna, northwest of Port Augusta, *Hilton 781* (ADW). A plant of this species is mounted with a probable isotype of *M. sphaerocarpa* from Mt. Olga in the Northern Territory (K) but there is no evidence that the plant was collected there.

The range of *Menkea crassa* overlaps, in part, that of *M. australis, M. sphaerocarpa* and *M. villosula,* but this species can be recognized by the combination of stout stems and subsucculent foliage with white or cream-colored petals and glabrous inflated siliques. In South Australia, *M. lutea* is so far known only from the far northwestern part of the state, slightly beyond the known range of *M. crassa;* the former species is distinguished by bright yellow petals and compressed siliques. As mentioned in the discussion of *M. australis,* Max Koch confused that species and this one, and his number 270, widely distributed as the "typical form" of *M. australis,* is *M. crassa. Menkea crassa* seems most closely related to *M. villosula* which it resembles in that the stems are frequently erect, the siliques are inflated and the septum is not entirely absent.

6. **Menkea sphaerocarpa** F. Muell., Fragm. 8:223. 1874
Map 2

HOLOTYPE: Northern Territory. Mt. Olga: *E. Giles*, 1873 (MEL 7674). The following sheets include material which may be isotypes or parts of the type: AD (ex Herb. Ralph Tate), K (these two sheets both labelled "Mt. Olga," but lacking date and collector's name), MEL 7682, MEL 7683 (both sheets unlabelled, but on the latter is an annotation made by Mr. J. H. Willis of the National Herbarium of Victoria suggesting that the material might be part of the type).

Plant an erect or prostrate glabrous annual; stems 1.5–3 dm. long, usually branched, often with much reddish or purplish pigmentation; basal leaves to 7 cm. long and 12 mm. wide, the blades obovate to spathulate, usually coarsely lobed or dentate, tapering to a slender petiole often as long as the blade; cauline leaves few, 1.5–4 cm. long, 5–12 mm. wide, obovate to spathulate, sometimes falcate, entire or shallowly dentate, sessile or (the lowermost) on a short petiole; inflorescences initially dense, but soon elongating, buds subglobose; sepals 2.1–3.1 mm. long, elliptic to oblong or ovate, sometimes cucullate; petals 3.0–5.2 mm. long, 2.0–4.5 mm. wide, pink to mauve, or white (but often drying yellow), the blades orbicular to (ob-)ovate and narrowing suddenly to the broad claw; stamens 2.1–3.1 mm. long, the filaments dilated at the base; glandular tissue pentagonal or hexagonal around the single stamens and subtending the paired ones, sometimes developed between the latter; ovules 25–70 per locule; infructescences loose, to 10 cm. long; pedicels 5–15(–20) mm. long, usually spreading but sometimes erect or horizontal; siliques 3–7 mm. long, 1.0–3.5 mm. wide, subglobose to ellipsoid or obovoid and slightly compressed, sessile or on a short stipe; styles 0.6–1.0 mm. long and slender, the stigmas depressed-capitate; septum obsolete; seeds 0.3–0.5 mm. long, ellipsoid to oblong, dark brown to dark red-brown; cotyledons slightly shorter than the radicle.

REPRESENTATIVE SPECIMENS: **Northern Territory.** 22 miles west of Victory Downs Homestead, *George 5103* (PERTH). **Western Australia.** Giles road, 4 miles south of Blackstone turnoff, *George 5218* (PERTH); Brockman River, west of Carnegie, *George 5574* (PERTH); 25 miles west of Wiluna, *Gardner 2379* (PERTH); Lake Miranda, edge on sand, 21 miles north of Agnew, on road to Wiluna, *Aplin 2370* (PERTH); East of Laverton, Geological Survey no. 49 (PERTH); Parker's Range, *Merrall* (MEL 7684). **South Australia.** 42 miles south of Mt. Davies camp, Tomkinson Range, *Symon 2531* (AD, ADW); Ernabella Mission Station, Musgrave Ranges area, *Coombe*, 1955 (AD, MEL 7672, 7673, NSW 77556); between camps 10 and 11 [of the Elder Exploring Expedition, i.e., between the Birksgate and Everard Ranges], *Helms*, 1891 (AD, K, MEL 7675, 7679, NSW 77558); 9 miles east of Emu Clay Pans, *Forde 350* (AD, CANB, MEL 7671).

The material on the holotype sheet consists only of silique valves and a few fragments of stem, but Mueller referred to *Menkea sphaerocarpa* as "speciem pulchellam et eximiam" and the protologue includes details of leaves and flowers which may have been drawn from material on MEL 7683, one plant on this sheet having a few flowers and leaves. However, MEL 7674 must

be regarded as the holotype for it is the only sheet of this species at the National Herbarium of Victoria which can be connected with certainty to Mt. Olga and Ernest Giles.

This sheet is labelled "1873–1874," referring to Giles' second expedition into central Australia and the collection was probably made during the third week of September, 1873, when Giles and his companions spent a few days near the base of Mt. Olga to rest their horses. In Australia Twice Traversed (vol. 1, p. 292), Giles remarked, ". . .just about Mt. Olga I fancied I had discovered several new species." and, in fascicle 69 of Fragmenta Phytographiae Australiae, published soon after Giles' return to the settled areas, Mueller described, among others, five species from Mt. Olga or nearby.

In South Australia *Menkea sphaerocarpa* occurs in the northwest and seems not to have been collected east of the Everard Ranges. Mueller and Tate (1896), in enumerating the collections of the Elder Expedition, refer to this species collections made on the Cootanoorina and Arkaringa Creeks, while J. M. Black (1917) cited Lake Blanche and Mt. Lyndhurst and, in 1918, "waterhole near Marree." With the exception of Arkaringa Creek, which is northwest of Ooodnadatta, these are places in northeastern South Australia, and the collections all belong to *M. crassa*.

LITERATURE CITED

Bentham, G. 1863. Flora Australiensis. vol. 1. London.

Black, J. M. 1917. Results of the South Australian Museum Expedition to Strzelecki and Coopers Creeks. (o) Botany. Trans. Roy. Soc. S. Austral. **41**:405–658.

————————. 1918. Additions to the flora of South Australia. No. 14. Trans. Roy. Soc. S. Austral. **42**:168–184.

Giles, E. 1889. Australia Twice Traversed. 2 vols. London.

Lanjouw, J. and F. A. Stafleu. 1964. Index Herbariorum. Part I. The Herbaria of the World. ed. 5. Regnum Vegetabile. vol. 31. Utrecht.

Lehmann, J. G. C. (ed.) 1844–1848. Plantae Preissianae. Hamburg.

Mueller, F. and R. Tate. 1896. Scientific Results of the Elder Exploring Expedition. Botany (Phanerogams and Vascular Cryptogams). Trans. Roy. Soc. S. Austral. **16**:333–383.

Schulz, O. E. 1924. *Cruciferae-Sisymbrieae*. Das Pflanzenreich **86**:1–388.

————————. 1933. Kurze Notizen über neue Gattungen, Sektionen und Arten der Cruciferen. Englers Bot. Jahrb. **66**:91–102.

————————. 1936. *Cruciferae*. pp. 227–658 in A. Engler & K. Prantl, eds. Die natürlichen Pflanzenfamilien, Auf. 2. Band **17b**. Leipzig.

Shaw, E. A. 1965. Taxonomic Revision of some Australian Endemic Genera of *Cruciferae*. Trans. Roy. Soc. S. Austral. **89**:145–253.

NOTES ON STREPTANTHUS AND ERYSIMUM (CRUCIFERAE)

Reed C. Rollins

The preparation of a taxonomic treatment of the *Cruciferae* for the projected manual of the flora of Texas by Donovan S. Correll and Marshall C. Johnston has required the careful examination of species identities in all genera known to occur in the state. Material of an undescribed species of *Streptanthus* was provided among the specimens collected by Correll and his associates during the past few years. A key to the species of *Streptanthus* of Texas is followed by a description of the new species.

Upper cauline leaves petiolate or at least cuneate at base.
  Cauline leaves entire, cuneate at base to short-petioled; petals equally developed ..... *S. hyacinthoides.*
  Cauline leaves runcinate, long-petioled; petals unequal, lower petals with blades absent or poorly developed ..... *S. cutleri.*
Upper cauline leaves auriculate and clasping the stem.
  Petal blades well developed, showy, at least twice as wide as the claw.
    Lower cauline leaves auriculate.
      Siliques less than 2.5 mm. wide; lower cauline leaves entire or at most shallowly sinuate-dentate ..... *S. maculatus.*
      Siliques 5–6 mm. wide; lower cauline leaves pinnatifid to somewhat lobed ..... *S. sparsiflorus.*
    Lower cauline leaves petiolate.
      Infructescences fully bracteate; mature pedicels terete; siliques less than 3 mm. wide ..... *S. bracteatus.*
      Infructescences ebracteate or the lower pedicels infrequently subtended by bracts; mature pedicels angular, striated; siliques 4–6 mm. wide ..... *S. platycarpus.*
  Petal blades poorly developed, not showy, about the same width as the claw ..... *S. carinatus.*

Streptanthus sparsiflorus Rollins sp. nov.

Herba annua; caulibus erectis ramosis 3–6 dm. altis; foliis inferne sessilibus auriculatis pinnatifidis 8–12 cm. longis, 2–4 cm. latis; foliis caulinis superne ovatis amplexicaulibus glaucis integris vel sinuatis; floribus sparsis purpureis; pedicellis divaricatis vel adscendentibus glabris 5–10 mm. longis; siliquis adscendentibus vel erectis glabris subsessilibus 4–7 cm. longis, 5–7 mm. latis; seminibus orbicularibus alatis ca. 5 mm. latis; cotyledonibus accumbentibus.

Holotype in the Gray Herbarium: south fork of McKittrick Canyon, Guadalupe Mts., Culberson County, Tex., June 21, 1964, *D. S. Correll* 29805 and *Craig Hanson*. Isotype in the Lundell Herbarium, Texas Research Foundation.

Annual herb, glabrous throughout, stems and leaves glaucous, somewhat fleshy; leaves greenish and minutely puncticulate above, slate-colored and

non-puncticulate below, strictly radical leaves absent; stems 3–6 dm. tall, simple below, branched from about 1 dm. upward; lower cauline leaves sessile, auriculate, repand-toothed, lyrately pinnatifid to nearly runcinate, 8–12 cm. long, 2–4 cm. wide, leaves gradually reduced upward; upper cauline leaves mostly entire, occasionally sinuate-dentate, ovate to broadly oblong, obtuse, auriculate and clasping the stem; flowers usually fewer than 10 per raceme, slightly irregular; sepals straw-colored to pale purplish, non-saccate, narrowly ovate, 9–11 mm. long, ca. 2 mm. wide, lateral sepals more tapering and thicker at tip than upper and lower sepals; petals showy, purplish 15–18 mm. long, blades 3–5 mm. wide, reflexed at anthesis; upper paired stamens protruding beyond sepals, filaments 7–9 mm. long, anthers 2.5–3 mm. long; lower paired anthers included within calyx, filaments 4–5 mm. long, anthers 3–4 mm. long; single stamens often with anthers longer than filament; fruiting pedicels stout, terete, divaricately ascending, 5–10 mm. long, strongly expanded at summit; siliques subsessile, divaricately ascending, linear, obtuse to nearly acute above and below, strongly flattened parallel to septum, 4–7 cm. long, 5–7 mm. wide; valves with a central nerve from base to apex; septum translucent, entire; funiculi winged; seeds flattened, widely wing-margined, orbicular, about 5 mm. across, wing uniform, 1–1.2 mm. wide, crest bilobed, primary cleft short, less than 0.5 mm. long; cotyledons accumbent.

OTHER SPECIMENS STUDIED: Pine Springs Canyon, Guadalupe Mts., June 20, 1964, *Correll* 29793 and *Hanson* (GH, LL); same locality *Correll 24270* and *M. C. Johnston* (GH); same locality, *Correll* 26088 and *H. B. Correll* (LL).

Specimens of *Streptanthus sparsiflorus* were at first identified as S. *platycarpus* primarily because of the presence of broad-bladed petals. However, in most respects, this species is more similar to S. *carinatus* than it is to S. *platycarpus*. All three species have similar broad siliques borne on stout pedicels, but the pedicels of S. *sparsiflorus* and S. *carinatus* are short, more nearly terete and they are always glabrous, whereas those of S. *platycarpus* are long, less definitely terete and almost always possess at least a few simple trichomes.

Aside from the broad flat petal blades present in *Streptanthus sparsiflorus* as compared with narrow linear and undulate-crisped blades of S. *carinatus*, the most striking difference between these two species is in the lower leaves. The lower leaves of S. *carinatus* are definitely petioled and non-auriculate, while in S. *sparsiflorus*, the lower leaves are sessile and auriculate. Also, there are differences between the two species in flower and bud color. The buds of S. *carinatus* are a very dark purple, almost blackish in some plants, and the petal blades are usually dirty white streaked with purple veins, only very rarely purplish. On the other hand, the buds of S. *sparsiflorus* are mostly straw-colored, rarely somewhat purplish

and the blades are definitely purple-violet. The calyx in the newly opened flower of *S. carinatus* is urn-shaped and very definitely asymmetrical with the upper and lower sepals gibbous below the middle. The calyx and sepals of *S. sparsiflorus* do not appear to be urn-shaped and gibbous, but we have not seen growing material of this species and we do not have a sufficient range of stages in our specimens to be certain about these points.

Streptanthus carinatus and *S. sparsiflorus* are similar in possessing protruding upper stamens which have short anthers, and with the lower paired stamens having longer anthers nearly included (cf., Rollins, 1963, Fig. 3 and 4). In contrast to this, both the upper and the lower pair of stamens in *S. platycarpus* are about of equal length and are nearly included. In the latter species, the anthers are very long, usually exceeding the filaments in length. Other interesting differences between *S. platycarpus* and the other two species are seen in the seed and funiculus. The funiculus in *S. platycarpus* is embedded in the septum and the attachment point on the seed is oriented toward the cotyledons rather than the primary groove. In *S. sparsiflorus* and *S. carinatus*, the funiculus is nearly free of the septum but is winged with tissue similar to that of the septum. In these species, the orientation of the funicular attachment is toward the primary groove of the seed.

Erysimum

The genus *Erysimum* is widespread in North America, especially if the adventive species are taken into account. Certain species, such as *E. capitatum*, are extremely abundant in the mountain and valley region which comprises much of the western half of the continent. However, the area of most active evolutionary differentiation in North America is very near the western coast especially from southern Oregon southward to Baja California and on the offshore islands. This point was brought out by Rossbach (unpublished thesis, Stanford University) and may be inferred from his abbreviated presentation in Aliso (Vol. 4: 115–124, 1958) where five new taxa from the coastal area were described.

Species of *Erysimum* have become adapted to the specialized habitats of coastal dunes in a number of instances and to serpentine rock detritus in others. Sandy soils of hillsides and open areas of chaparral and woodland are favorite sites in this coastal

region. Although uncommon in the genus as a whole in North America, a suffrutescent habit is well developed in *E. insulare* and to a lesser extent in *E. suffrutescens*, but material of an undescribed species from Guadalupe Island off the coast of Baja California shows an even higher level of woodiness than either of these species and represents, in this respect, an evolutionary extreme in the North American species of the genus. This new species is described as follows.

Erysimum moranii Rollins, sp. nov.

Planta suffruticosa ramosa 2–4 dm. altis; foliis integris crassis imbricatis dense pubescentibus lineari-oblanceolatis vel anguste spathulatis obtusis 1.5–3.5 cm. longis; petalis spathulatis luteis 7–9 mm. longis; pedicellis rectis pubescentibus divaricatis 3–5 mm. longis; siliquis rectis divaricatis compressis dense pubescentibus 2–3 mm. longis; seminibus brunneis alatis compressis ca. 2.5 mm. longis, ca. 2 mm. latis; cotyledonibus accumbentibus.

Holotype in the Gray Herbarium: occasional on inner slopes of the crater, ca. 50 m., Outer Islet, near 28.51′ N, 118.17′ W., Guadalupe Island, Baja California, Mexico, 21 June 1968, *Reid Moran 15116.*

Plants sub-shrubby, repeatedly branched, up to 4 dm. high, major stems up to 1 cm. in diameter; active leaves at the ends of branches or toward the base of the inflorescences, marcescent leaves extending well below the active ones; leaves entire, crowded, linear-oblanceolate to narrowly spatulate, gradually narrowing below, obtuse at apex, 1.5–3.5 cm. long, silvery from a dense covering of appressed bifurcate trichomes; flowering branches numerous, quadrangular, densely pubescent; fruiting pedicels slender, straight, widely spreading nearly at right angles to rachis or slightly ascending, densely pubescent, 3–5 mm. long; sepals densely pubescent, oblong, outer pair keeled on back and with a callus, at apex, enclosing inner pair; petals yellow, spatulate, 7–9 mm. long, gradually narrowing to a slender claw; siliques straight, flattened parallel to septum, widely spreading nearly at right angles to slightly divaricately ascending, 2.5–3.5 cm. long, ca. 3 mm. wide; valves densely pubescent, strongly nerved from base to apex; replum narrow, pubescent; styles capitate, sparsely pubescent, 2–3 mm. long; septum with areolae elongated parallel to long axis, obscure nerve narrow but extending full length of septum; seeds wing-margined all around, flattened, slightly longer than broad, ca. 2 mm. wide and 2.5 mm. long, lateral wing ca. 0.25, slightly wider on distal portion of seed; radicle exceeding cotyledons; cotyledons accumbent. $2n=36$.

OTHER SPECIMENS SEEN: occasional on inner slope, Outer Islet, Guadalupe Island, Baja California, Mexico, April 16, 1948, *Reid Moran* 2935 (DS); floor of crater on Outer Islet, Guadalupe Island, July 18–19, 1937, *Peter J. Rempel s.n.* (DS).

The Outer Islet is also known as Islote Zapato and according to Moran (1969) it consists mostly of a seabound volcanic crater with steep inner slopes and sheer outer seacliffs on three sides.

It is noteworthy that Moran found and described a new species of *Eriogonum (E. zapatoense)* from the same location.

In its shrubby habit, *Erysimum moranii* is most like *E. insulare* and *E. suffrutescens*. However, it differs from each of these species in a number of significant ways, one of the most important being in the nature of the seeds. In *E. moranii*, the seeds are broad, flattened, winged all around and the cotyledons are accumbent while in *E. insulare* they are narrow, plump, wingless and the cotyledons are incumbent. These two species also differ in the length of the pedicels and siliques, the pedicels being 1.5–2 cm. and the siliques 3–5 cm. in *E. insulare* compared to 3–5 mm. and 2.5–3.5 cm. in *E. moranii*.

Actually, *Erysimum moranii* may be more closely related to *E. suffrutescens*, particularly var. *grandifolium*, than it is to *E. insulare*. However, these species differ considerably in growth habit, leaf disposition and leaf length. The pedicel length is somewhat comparable, although usually shorter in *E. moranii* and the silique length of var. *grandifolium* is about the same or slightly longer than in *E. moranii*. The siliques of var. *grandifolium* are definitely tetragonal in cross section whereas they are broader and flat in *E. moranii*. The seeds of these taxa are radically different being plump, angular, wingless and with mostly incumbent cotyledons in var. *grandifolium*, but flat, nonangular, winged and with accumbent cotyledons in *E. moranii*. Furthermore, the trichomes of *E. moranii* are consistently two parted while being three parted in all infraspecific taxa of *E. suffrutescens*.

Plants grown in a growth chamber from seeds of the type number began branching after a few weeks of growth and continued to ramify into a bush-like form as growth proceeded. This growth habit is substantially different from that of many species of *Erysimum* (e.g., *E. capitatum, E. asperum et al.*) where a single rosette of leaves is most common and if branching does occur it is usually in the upper part of the flowering stalk. Actually, the growth-form is more like that of some of the Aegean species of *Erysimum* (cf., Snogerup, 1967a) which are also island dwellers.

The chromosome number[1] of $2n=36$ in *Erysimum moranii* is the same as in a number of other North American species of the genus (Mulligan, 1966; Rollins, 1966). There are both large

[1] I am indebted to and wish to thank Mrs. Lily Rüdenberg for this count and for the privilege of examining preparations of root-tip smears of *E. moranii*.

and very small chromosomes in the complement of this species and in this respect the cytological picture is similar to that of other American species as well. The range of chromosome size is far greater than in any complement of the Aegean species of *Erysimum* as given by Snogerup (1967b).

LITERATURE CITED

MULLIGAN, G. A. 1966. Chromosome numbers of the family *Cruciferae*. III. Canad. Journ. Bot. **44**:309–319.

ROLLINS, R. C. 1963. Protandry in two species of *Streptanthus (Cruciferae)*. Rhodora **65**:45–49.

———. 1966. Chromosome numbers of *Cruciferae*. Contrib. Gray Herb. **197**;43–65.

SNOGERUP, S. 1967a. Studies in the Aegean flora VIII. *Erysimum* sect. *Cheiranthus* A. Taxonomy. Opera Botanica No. 13:1–70.

———. 1967b. Studies in the Aegean flora IX. *Erysimum* sect. *Cheiranthus* B. Variation and evolution in the small-population system. Opera Botanica No. 14:1–86.

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PROTOGYNY IN THE CRUCIFERAE AND NOTES ON ARABIS AND CAULANTHUS

REED C. ROLLINS

Since my early works on *Arabis* (Rollins 1936, 1941), I have grown many species of the genus and studied more than a score of North American species in flower in the greenhouse or experimental garden. However, none of these showed any evidence of functional protogyny and none had excerted anthers. Now, flowering material of the taxon I have previously called *Arabis suffrutescens* var. *perstylosa* shows both protogyny and excerted anthers to be present. When buds are fully grown and just before anthesis, the elongating style projects through the apex of the slightly opened bud exposing the stigma. This is clearly shown in the left hand photograph of Plate 1. After pollination, the style tends to bend to one side of the flower and the filaments elongate until the anthers of the paired stamens are well excerted above the corolla. Even the anthers of the shorter single stamens are above the ends of the petals when the flower is at full anthesis. The anther position is shown in the right hand photograph of Plate 1. Tests on three plants show them to be self-incompatible. This is taken as reasonably good evidence that the taxon as a whole is essentially self-incompatible.

Protogyny is not supposed to be present in the *Cruciferae* (Bateman 1955a) and even now we assume it is not common in this family or its occurrence would have been noted in the literature. Such a modification of the usual maturation sequence within the flower promotes outcrossing and is of significance for the survival of a population if there is a reduced gene pool and if other outcrossing mechanisms are not present or are ineffective by themselves.

The *Arabis* population from which our seeds were obtained apparently is a small localized one and there is some circumstantial evidence that this taxon itself is very restricted in numbers of populations, possibly consisting of a single population of a limited number of individuals. Only two collections of it have been made, both by Professor Lincoln Constance of the University of California at Berkeley. He made the first collection, in 1938, which was used as the basis for describing the new taxon, *A. suffrutescens* var. *perstylosa*. In 1969, Dr. Constance, accompanied by T. I. Chuang, made a second collection at the same site as the first, including mature seeds from which our plants were grown. At that time a considerable search of the area was made without the discovery of any new sites.

The one known population is on an open serpentine outcrop near rocks. Other crucifers, particularly taxa of the genus *Streptanthus*, occupy similar serpentine habitats (Kruckeberg 1951, 1954, 1957) and are often equally limited in their distributions. In the case of the *Arabis* here being con-

PLATE 1. *Arabis constancei*. Left, bud with projecting style. Right, flower at full anthesis. Both figures × 20. Photo by Frank White.

sidered, it is possible that the population has become too reduced in incompatibility allele number for self-incompatibility to function efficiently as an outcrossing mechanism. Selective pressure to promote outcrossing in some other way could be intense under such circumstances. The development of protogyny is one way the need for increased outcrossing could be insured by the population, if the incompatibility system became inefficient. It is interesting that new information has now completely negated the statement Bateman (*op. cit.*, p. 63) could make only a few years ago that, "there is no protandry, no protogyny and no dioecy in Crucifers." We have shown that protandry is present in two species of *Streptanthus* (Rollins 1963), dioecy was acknowledged to be characteristic of *Lepidium sisymbrioides* by Bateman (1955b), and now, protogyny is shown to be present in the family. There is evidence produced by one of my students, Mr. Ihsan Al-Shehbaz, that protogyny occurs in the genus *Thelypodium* and we now think it may be more widespread in the *Cruciferae* than we would have supposed at the time of our initial discovery of it.[1]

In the course of our study of the *Arabis* material referred to above, it has become clear that the taxon involved should be recognized on the specific level and not associated with *A. suffrutescens* as in my former treatment. Because of his involvement in obtaining the original, and subsequent collections, and his continued interest and help, I propose to name this species for my former mentor and long time friend, Dr. Lincoln Constance. Actually Dr. Constance and I published a new species of *Arabis* together [*A. crucisetosa*] many years ago (Constance & Rollins 1936).

Arabis constancei Rollins, sp. nov.

Herba perennis, caudicibus ramosis, caulibus simplicibus erectis glabris 1.5–3 dm. altis, foliis basilaribus integris glabris vel ciliolatis lineari-oblanceolatis 1.5–3 cm. longis, 2–3.5 mm. latis, foliis caulinis sessilibus non auriculatis glabris, sepalis glabris oblongis 3.5–4.5 mm. longis, ca. 2 mm. latis, petalis erectis anguste spathulatis albidis 5.5–7 mm. longis, staminibus erectis excertis filamentis elongatis, pedicellis recurvatis glabris 6–10 mm. longis, siliquis compressis glabris pendulis acutis vel accuminatis 4–5.5 cm. longis, 3–4 mm. latis, stylis 2.5–4.5 mm. longis, seminibus orbicularibus vel late ellipticis compressis alatis, cotyledonibus accumbentibus.

Holotype in the Gray Herbarium, collected near rocks on open serpentine. 7.6 miles southeast of Quincy on road to Blairsden, Plumas Co., California, July 11, 1969, *L. Constance & T. I. Chuang 3875*. Additional collection studied: open bare serpentine slope, above Middle Fork of the Feather River, 7.3 miles southeast of Quincy, Plumas Co., California, June 9, 1938, *L. Constance 2309* (GH).

Perennial; stems one to several from a branching subligneous caudex, erect, simple, wholly glabrous, 1.5–3 dm. high; basal leaves in dense rosettes, entire, linear-oblanceolate, acute, stiff, thickish, with a prominent mid-rib, bluish-green, ciliolate

[1]While the present paper was in process, an unpublished thesis entitled, "Investigations in the Floral Biology of the Arabis Holboellii Complex," by Thomas Frank Johnson was sent to me by Professor Arthur R. Kruckeberg. Johnson observed emergent pistils in *Arabis holboellii* and in *A. sparsiflora* which surely means that they are protogynous. Thus, we are certain of the prediction that protogyny is more common than we could have reasonably believed a few months ago.

on the margins with simple or forked trichomes to glabrous, 1.5–3 cm. long, 2–3.5 mm. wide; cauline leaves entire, oblong to lanceolate, sessile, non-auriculate, glabrous, reduced upward, overlapping below, remote above, 1–1.5 cm. long, 2–4 mm. wide; inflorescences 5–10–flowered, loose; flowers erect to divaricately ascending, nodding to reflexed after anthesis, sepals green, scarious-margined, glabrous, oblong, non-saccate or the outer pair slightly saccate, 3.5–4.5 mm. long, ca. 2 mm. wide; petals erect, narrowly spatulate, tapering gradually from blade to claw, 5.5–7 mm. long, white to off-white; stamens excerted, erect, introrse, filaments of paired stamens 7–8 mm. long, filaments of single stamens 6–7 mm. long, anthers ca. 1 mm. long; siliques pendulous to strictly reflexed, glabrous, strongly flattened, nearly straight but with uneven margins, nerved from base to middle or slightly above, acute to accuminate at apex, 4–5.5 cm. long, 3–4 mm. wide; styles 2.5–4.5 mm. long; fruiting pedicels strongly reflexed but not geniculate, glabrous, 6–10 mm. long; seeds flattened, nearly orbicular to slightly oblong, winged except for area of funicular attachment, ca. 3 mm. in diameter including wings; wing ca. 0.5 mm. wide; cotyledons accumbent; radicle separated from cotyledons by a deep groove. $2n = 14$.

There is no doubt that *Arabis constancei* is a close relative of A. *suffrutescens*. However, the exposed differences betwen these taxa have been increased in number as we have had more material to work with, particularly growing plants, from which we could make comparisons of characters. The sharpest differences are in the flowers which we did not have available for study at the time of our former treatment of this taxon.

Previously, we had indicated the plants of *Arabis constancei* to be wholly glabrous. But the new specimens of this species show the basal leaves frequently to be ciliolate-margined. If the leaves become glabrate, then there often is one or a few trichomes at the apex of the leaf. For some reason, the specimens of the earlier collection, *Constance 2309*, were wholly glabrous. This is also true of the plants we grew in the greenhouse even though the seeds were from wild plants which had at least some trichomes on their basal leaves.

Arabis constancei differs from *A. suffrutescens* in having non-auriculate instead of auriculate cauline leaves, greatly elongated styles instead of sessile stigmas or at most very short styles, excerted stamens rather than included stamens and seeds with wings about 0.5 mm. wide rather than 1 mm. wide. In general, there is less of a woody foot present in *A. constancei* than in *A. suffrutescens*. Also, there is a much better developed basal rosette with a denser cluster of leaves in the former than in the latter. In any given plant of *A. constancei* usually there are both fertile branches and sterile branches present. But in *A. suffrutescens*, sterile branches are not present or are exceedingly rare.

Caulanthus

At various times over the past thirty years, I have considered the generic problem posed by a strong similarity of several species, some of which are usually treated in the genus *Streptanthus* and others that are ordinarily placed in *Caulanthus*. Might not all these species be better put under *Streptanthus*, the older of the two names, as was done by Jepson (1936)? In setting up the genus *Caulanthus*, Watson (1871) was impressed by the

need to separate from *Streptanthus* a group of species having seeds with incumbent cotyledons, mostly terete to slightly obcompressed siliques and petals with reduced blades. He left to *Streptanthus* those species with siliques strongly flattened parallel to the septum, seeds with accumbent cotyledons and petals with developed blades. Greene (1904) strongly dissented from the treatment of Watson and a later one of Robinson (1895), but by proposing nine new genera to include the species mostly to be associated together in *Streptanthus* and *Caulanthus*, he was hardly of any help in developing a reasonable classification for the group. Payson (1923) provided an important presentation of the problem and of a classification that was more or less in accord with the treatment of the earliest authors. His monograph has helped to establish *Caulanthus* in the manuals and floras and I believe this is nearer the mark than would be a return to a more inclusive *Streptanthus*. However, we are quite aware that *Streptanthus* and *Caulanthus* illustrate once again one of the most frequently encountered problems in the taxonomy of the family *Cruciferae*, that of indistinct boundaries separating the genera. In my judgment, it is in the interest of a reasonable and workable classification to accept both *Caulanthus* and *Streptanthus*.

It was necessary to review this matter and arrive at a decision in order to be able to handle the identities of certain specimens received from several areas in the intermountain basin. For the present, I shall deal with one new taxon that falls clearly into the genus *Caulanthus*. However, since Jones (1893) referred to specimens of it in the protologue of the original description of *Thelypodium elegans*, it is first necessary to point out that although the species described below resembles *T. elegans* [*Sisymbrium elegans* (Jones) Payson] in a general way, the two taxa are very distinct. I have examined the holotype and three isotypes of *T. elegans*. These are consistent with the description insofar as the characters of the plants are concerned and differ only with respect to the minor fact that the labels all read May 6, 1891 instead of May 7, 1891 as given in the protologue. Attached to the holotype is a card giving the description in Jones' handwriting, largely as he published it. However, two collections with the same data as the type series, "Westwater, Colo., May 6, 1891, collected by Marcus E. Jones, A.M.," one at California Academy of Sciences and one at the Gray Herbarium, are similar to specimens from Green River, Utah, referred to below and do not belong to the type series. It is assumed that there was some mixing of two collections before they were distributed, perhaps by Jones himself. In the protologue, Jones states "A form from Green River, Utah, that I refer to this species is simple stemmed and with appressed pods." Two collections from the Jones herbarium in the Pomona College herbarium dated May 7, 1891 and May 9, 1890 from Green River, Utah, undoubtedly represent the material mentioned. These and several more recent collections from the Green River area belong to *Caulanthus divaricatus* rather than to *Sisymbrium elegans*.

Caulanthus divaricatus Rollins, sp. nov.

Herba annua, caulibus erectis simplicibus vel superne ramosis 2–9 dm. altis inferne pubescentibus vel glabratis superne glabris ramis divaricatis, foliis inferne integris vel dentatis sessilibus non-auriculatis oblongis obtusis glabris vel sparse pubescentibus 4–10 cm. longis, 1–3 cm. latis, foliis superne auriculatis ovatis imbricatis glabris 2–8 cm. longis, 1–2 cm. latis, sepalis erectis non-saccatis ochroleucis 3.5–4 mm. longis, petalis ochroleucis vel inferne albidis 7–9 mm. longis, antheris sagittatis ca. 1.5 mm. longis, pedicellis divaricatis tenuibus glabris vel sparse pubescentibus 7–12 mm. longis, siliquis teretibus divaricatis glabris vel sparse pubescentibus 6–9 cm. longis, stylis clavatis 1.5–2 mm. longis, seminibus oblongis immarginatis 1.5–2 mm. longis, cotyledonibus incumbentibus.

Holotype in the Gray Herbarium collected about 75 miles west of Blanding and 10 miles east of Hite, Twp. 34 S. R. 14 E., San Juan Co., Utah, May 16, 1961, *Arthur Cronquist 9033*. Isotype NY.

Plants annual, single stemmed and without a true basal rosette of leaves; stems erect, virgately branched above, rarely simple, densely pubescent below with contorted and twisted whitish flat trichomes to nearly glabrous, usually glabrous above, 2–9 dm. high; lowest cauline leaves densely overlapping, sessile but scarcely auriculate, entire to irregularly dentate, oblong, obtuse, strongly 1-nerved, sparsely pubescent to glabrous 4–10 cm. long, 1–3 cm. wide; cauline leaves becoming strongly auriculate upward from the lowest members, upper leaves less closely overlapped, more ovate in shape and more acute than the lower; all branches terminated by dense inflorescences; flower pedicels divaricately ascending, slender, sparsely pubescent to glabrous; sepals erect scarcely saccate to non-saccate ochroleucous 3.5–4 mm. long; petals erect, strongly nerved, 7–9 mm. long; claw whitish, obovate, abrupty narrowed at blade junction, 4–5 mm. long, ca. 2 mm. wide; blade vertically folded and crisped, yellowish, 3–4 mm. long, ca. 1 mm. wide; filaments erect, 4–4.5 mm. long; anthers slightly excerted, sagittate, introrse, not coiled, ca. 1.5 mm. long; paired stamens only slightly longer than single stamens; mold of glandular tissue subtending base of paired filaments, nearly encircling single filaments except for an area below filament insertion; ovary terete, usually very sparsely pubescent; stigma slightly larger in diameter than style, slightly bilobed, the lobes over the replum margin; fruiting pedicels divaricately ascending to more widely spreading, straight, slender, sparsely pubescent to glabrous, 7–12 mm. long; siliques terete, straight, nearly erect to divaricately ascending or more widely spreading as the plants mature, sparsely pubescent to glabrous, 6–9 cm. long, nearly sessile to gynophorate, gynophore, if present, up to 1 mm. long; valves strongly 1-nerved and with 2 weaker secondary nerves; styles subclavate, 1.5–2 mm. long, ca. 1 mm. wide, wingless or with a minor distal wing-like projection; cotyledons incumbent. Plate 2.

There is some variation represented by the specimens cited below but most of this appears to be uncorrelated. The differences such as glabrous vs. pubescent individuals are present in the same populations as are differences in the length of the gynophore. The position of the pedicels and of the siliques appears to be related to maturity. Both pedicels and siliques are nearly erect in the earlier stages becoming more widely spreading as the infructescences mature.

Caulanthus divaricatus has flowers that are yellowish in overall appearance because the sepals, short petal blades and anthers are yellow to straw colored. However, the claw of the petal which is included within the calyx is much lighter and in living material we have in the greenhouse this part of the petal is nearly white. In dried specimens, the same appears to be true. The broad claw which abruptly narrows to a constriction at the junction of the crisped blade is a feature of most species of *Caulanthus* and

PLATE 2. *Caulanthus divaricatus*. Photo of the holotype, × 2/3. Photo by Frank White.

serves to distinguish this species from others in *Sisymbrium* with which it might otherwise be confused.

OTHER COLLECTIONS STUDIED. **Utah Carbon Co.:** 2 miles n. of Price, *D. E. Bright 10* (BYU); Price, *S. Flowers 1438, 1438a* (UT). **Emery Co.:** 1 mile n. of Castle Dale, *Bassett Maguire 18334* (NY); about 10 miles east of Huntington, *Higgins & Reveal 1256* (GH, NY); Clawson, *Ripley & Barneby 4735* (CAS, GH); 3 miles n. of Woodside, *S. L. Welsh 6887* (BYU, NY); Gunnison Butte, *O. S. Walsh 31* (UT); 1 mi. s. of jct. 24 & Notom Rd., R. 7 E., T. 30 S., *Atwood 1255* (GH). **Grand Co.:** Westwater,[2] May 6, 1891, *M. E. Jones s. n.* (CAS, GH); Grand River near Moab, June 3, 1915, *M. E. Jones s. n.* (GH); Cisco, May 6, 1891, *M. E. Jones s.n.* (UC); Green River, May 7, 1891, *M. E. Jones s.n.* (POM); same, May 9, 1890 (POM, UC); same, May 23, 1914 (CAS, MICH, POM); 10 Mile Creek, near Green River, May 26, 1915, *M. E. Jones s.n.* (CAS, F, NY, UC). **Wayne Co.:** about 29 miles southwest of Hanksville, *Arthur Cronquist 8934* (GH, NY). **Garfield Co.:** about 25 miles s. of Hanksville, *Welsh, Atwood & Higgins 8953* (BYU). **San Juan Co.:** Whirlwind Draw, R. 15 E., T. 39 S., *H. Rooney 245* (BYU).

[2]Not "Colo" meaning the state of Colorado as would be assumed from the way the label is written and as was given by Jones in his citation of the type of *Thelypodium elegans*. A clue to this mistake is found in Jones' handwritten note on one of the sheets in which he says, "Westwater on the Colo.," meaning the Colorado River. Westwater is in Utah, although it is near the Colorado border.

LITERATURE CITED

BATEMAN, A. J. 1955a. Self-incompatibility Systems in Angiosperms III. *Cruciferae*. Heredity **9**: 53–68.

————————. 1955b. Note on Dioecy in the *Cruciferae*. Heredity **9**: 415.

CONSTANCE, L. AND R. C. ROLLINS. 1936. New or otherwise Noteworthy Northwestern Plants II. Two New Species from the Grand Canyon of the Snake River. Proc. Biol. Soc. Wash. **49**: 147–150.

GREENE, E. L. 1904. Certain West American *Cruciferae*. Leaflets Bot. Obs. and Crit. **1**: 81–90; cf., 224–229.

JEPSON, W. L. 1936. A Flora of California **I**: 20–35.

JONES, M. E. 1893. Contributions to Western Botany. No. 5. Zoe **IV**: 254–282.

KRUCKEBERG, A. R. 1951. Intraspecific Variability in the Response of Certain Native Plant Species to Serpentine Soil. Amer. Journ. Bot. **38**: 408–419.

————————. 1954. The Ecology of Serpentine Soils. III. Plant Species in Relation to Serpentine Soils. Ecology **35**: 267–274.

————————. 1957. Variation in Fertility of Hybrids between Isolated Populations of the Serpentine Species, *Streptanthus glandulosus* Hook. Evolution **XI**: 185–211.

PAYSON, E. B. 1923. A Monographic Study of *Thelypodium* and Its Immediate Allies. Ann. Mo. Bot. Gard. **9**: 233–324.

ROBINSON, B. L. 1895. *Cruciferae*. Gray and Watson, Synoptical Flora of North America **1**: pt. 1. 98–180.

ROLLINS, R. C. 1936. The Genus *Arabis* L. in the Pacific Northwest. Res. Studies State Coll. Wash. **IV**: 1–52.

————————. 1941. A Monographic Study of *Arabis* in Western North America. Rhodora **43**: 289–325, 348–411, 425–485.

————————. 1963. Protandry in Two Species of *Streptanthus* (*Cruciferae*). Rhodora **65**: 45–49.

WATSON, S. 1871. Botany. U.S. Geol. Expl. Fortieth Parallel **V**: 14–31.

THE VASCULAR FLORA OF SAINT LAWRENCE ISLAND, WITH SPECIAL REFERENCE TO FLORISTIC ZONATION IN THE ARCTIC REGIONS

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INTRODUCTION

This paper consists of two sections: the first, a discussion of the vascular flora of St. Lawrence Island; and the second, a theoretical scheme for breaking the arctic regions of the world into a series of four floristic zones. This proposed system is an outgrowth of my fieldwork on St. Lawrence during the summers of 1966 and 1967, which also resulted in the treatment of the island's flora given in Section 1. When I first became interested in St. Lawrence Island, I was struck by the fact that less than 200 species of vascular plants were known to occur there, although some 500 or more species were known from areas on the adjacent mainland of Alaska. Since the Quaternary history of St. Lawrence is similar to that of the adjacent mainland areas, I assumed that the paucity of species reported from the island was simply the result of insufficient fieldwork. I fully expected to add 100 or more species to its known flora, particularly since many of the species that I expected to be the most common had never been collected there.

During my first summer's work on St. Lawrence, it soon became evident that the island's flora was, in fact, much more depauperate than that of any area of similar size on the adjacent mainland coast of Alaska. I was also surprised to discover that many species which were most abundant on the mainland coast were either missing entirely from the St. Lawrence Island flora, or were found only in a few isolated stations, usually in protected areas on the south side of the island. Clearly, the depauperateness of this flora must be largely due to currently acting ecological, rather than historical, factors. In this paper, it is shown that the main ecological factor is the amount of warmth available during the growing season. The majority of arctic vascular plant species have a northern limit of distribution which is in a state of equilibrium, controlled by the summer temperature regime of the area. On the basis of climatic data, it is possible to make quite accurate predictions of the composition of the flora of an area. Conversely, floristic data can be used to indicate the probable summer climatic regime of an area. A number of anomalous situations, such as the unusually rich flora of the Inner Fjord Region of Spitzbergen, can be explained on the basis of the concepts discussed in Section 2 of this paper.

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SECTION 1. THE VASCULAR FLORA OF SAINT LAWRENCE ISLAND

Location and History

Saint Lawrence Island lies in the northern portion of the Bering Sea, about 150 miles due south of the Bering Strait. Its location, in relation to adjacent mainland areas, can be seen on the map (Fig. 1). Although politically part of the State of Alaska, the island is geographically more closely related to Asia. On a clear day the jagged mountain ranges of the Chukchi Peninsula are clearly visible from the northwestern headlands of St. Lawrence as the Anadyr Strait, which separates the island from Cape Chaplino on the Siberian mainland, is less than 40 miles wide. One hundred and thirty miles of open sea separate St. Lawrence from the Alaskan mainland, which cannot be seen from the island under normal conditions of visibility. The Siberian affinities of St. Lawrence are nowhere more evident than with respect to the native human population of the island. Their Eskimo language is a branch of the Yupik dialect which is spoken only by the islanders and the natives of the adjacent coast of Siberia. In many other aspects of culture and physique, the St. Lawrence islanders show that their contact with other peoples has long been by way of Siberia (Giddings 1967).

Saint Lawrence Island lies some 200 miles south of the Arctic circle, at about the same latitude as Trondheim, Norway. Nevertheless, the environment of the island is truly arctic in every sense of the word. Low-lying areas are covered with dun-colored sedge tundra, while the hills are mostly barren rock and fell-field. The shrubby species which are so typical of the lush tundra of the Bering Sea coast of the Alaskan mainland occur only rarely on St. Lawrence, and the general aspect of the island is extremely bleak and barren. From November to June the island is locked in the grip of the polar ice pack, and dense fogs and high winds are of com-

FIG. 1. Map of the Bering-Chukchi Sea region. Approximate locations of 50 and 100 m isobaths shown by dotted lines. During periods of maximum glaciation, the shores of the Bering Land Bridge were in the vicinity of the present 100 m isobath.

mon occurrence throughout the year. Weather records indicate that the temperature regime of St. Lawrence is similar to that of Barentsburg, Spitzbergen, and Upernavik, at 75° north in high arctic West Greenland.

In sharp contrast to the barrenness of the land of St. Lawrence is the richness of the surrounding seas. Even today, after decades of overhunting, walrus, seal and whale are abundant during much of the year. The sea cliffs of the island support dense colonies of breeding sea birds which live on fish and crustaceans from the sea. The richness of the Bering Sea has allowed St. Lawrence Island to support a comparatively large human population for long periods of time, probably several thousand years. One can hardly travel a mile along the coast without seeing the remains of human habitations. There are several ancient village sites of magnificent proportions. The most impressive ones are built on a mound of their own rubbish rising to a height of 20 to 30 feet, and covering an area of several acres. The skulls of several hundred large whales can be seen on the surface of the abandoned village of Kialegak, and it is impossible to estimate the number of whales and walruses whose bones are buried in the huge mound. Instead of living the marginal, half-starved existence which many people believe to be the lot of the Eskimo, the inhabitants of Kialegak must have luxuriated in an abundant supply of fresh meat. An advantage of living in a cold climate is that meat can be kept relatively fresh in underground storage chambers for long periods of time. During the long nights, when a winter's supply of whale and walrus meat filled the meat cellars, the ancient islanders must have had plenty of time to dance to the monotone beat of the walrus-gut drums and to develop their art of carving the refractory walrus ivory.

Apparently the first European to learn of the existence of St. Lawrence Island was Vitis Bering, who sighted the island on August 10, (O.S.) 1728. Bering did not land; however, he did note the presence of "cottages of fishermen." He also gave the island its name, in honor of Saint Lawrence, on whose day the island was discovered. Many of the other early voyagers to Alaska came by way of the Bering Sea, and several of them made landfalls on the island. However, it did not prove to be a good source of valuable furs or precious metals, and was left more or less alone until the latter part of the 19th century, when the New England whalers began to hunt intensively in the Bering Sea. The islanders, well trained in the art of whaling, were soon being recruited as crew members. They also had large quantities of baleen and arctic fox furs for trade, and in later years some of the Eskimos became quite rich, even by white men's standards, prompting the disapproval of the resident missionaries.

However, the first prolonged contact between the white man and the St. Lawrence islanders was disastrous for the latter. The whalers' trade goods consisted largely of alcoholic beverages, and during the late 1870's the native population, weakened by excessive drinking, low on food, and probably suffering from an epidemic of some exotic disease, was dev-

estated. Villages which had been in existence for hundreds of years were so completely depopulated that the corpses were left unburied. At Kialegak it is still possible to find in the short, stiff tundra sedge which covers the village site, human skeletons lying where the bodies fell. By the time the naturalist, John Muir, arrived on the island aboard the *Corwin* in 1881, there were only about two hundred islanders left out of a population which may have been as high as 2000. The only village that survived with even a fraction of its population was Sevuokuk (Gambell) at Northwest Cape.

The white man came to St. Lawrence to stay about 1900, with the arrival of missionaries and schoolteachers at Gambell. At about the same time, reindeer were introduced to the island from Siberia. The best reindeer grazing lands proved to be the barren volcanic uplands of the Kookooligit Range in the central portion of the island, which supported a fairly heavy growth of the lichens that reindeer feed upon. To take advantage of the good grazing, the new village of Savoonga was founded on the north shore of the island, a short distance from the abandoned village of Kookoolik. Gambell and Savoonga are the only real villages on the island at present.

Anthropologists have long believed that the pre-Columbian inhabitants of North America reached the continent by way of the Bering Strait. Because St. Lawrence Island is so strategically located with respect to studies of the migration of early man across the Bering Land Bridge, the island has drawn a good deal of interest in archaeological circles, and excavations on the island began as early as 1930. Since then, extensive excavations at Gambell and Kookoolik have been made. There is no evidence at present regarding the existence of land bridge man, but numerous important discoveries of ancient Eskimo cultures have been made. Some of the carved ivory objects found on St. Lawrence represent the apex of Eskimo artistry and craftmanship (cf., Ray 1961; Giddings 1967).

With the onset of World War II and the Japanese occupation of the western Aleutian Islands, the military arrived on St. Lawrence, although never in great numbers. A number of small military installations, such as radar sites, were set up but most of these have subsequently been abandoned. A United States Air Force base at Northeast Cape is still in operation.

The native population of St. Lawrence Island is now about 1000 people, most of whom live in the villages of Gambell and Savoonga, although a small number also live near the Air Force base at Northeast Cape. Saint Lawrence is still one of the most isolated parts of Alaska, and the islanders have retained more of their traditional culture than have most Alaskan Eskimos. Much of the livelihood of the people is still based on the hunting of seal and walrus in the surrounding seas. The old houses of sod, driftwood and walrus hide have given way to small frame houses, many of which are a curious mixture of native and "white man"

architectural styles. The seal oil lamp has been replaced by gasoline and oil stoves, and the walrus skin boats are often powered by outboard motors, but the basic pattern of life on the island has been relatively stable until the present.

In general, the St. Lawrence islanders make relatively little use of the native plants of the island. A few species such as *Sedum rosea* are collected for food, while some others, notably *Angelica lucida,* are thought to have medicinal properties. The ethnobotany of the island is treated in detail in a separate paper (Young & Hall 1969).

Physiography and Geography

Saint Lawrence Island is about 100 miles long and varies in width from 10 to 40 miles. The total area of the island is roughly 2000 square miles, approximately equal to that of the State of Delaware. The eastern end of the island is a low, level plain punctuated by several ranges of block mountains, so that from the sea one has the impression of several separate islands. The western half of the island consists mainly of mountains and raised plateaus, with areas of low-lying plain being found only in a relatively narrow strip along the north coast, and along the north shore of the Koozaata Lagoon. The locations of the various physiographic features of the island are shown in Fig. 2.

The total length of the coastline of St. Lawrence is about 350 miles. About half of it consists of sandy barrier beaches which separate lagoons from the ocean; these beaches are normally from 100 yards to half a mile wide, and they seldom rise more than 20 feet above high tide line. The lagoons, enclosed by the barrier beaches, are often of considerable size. Koozaata Lagoon, the largest, is about 40 miles long and two to three miles wide. Most lagoons have a single outlet which normally discharges fresh water into the ocean, but during storms and periods of unusually high tide, salt water may back up into them or even wash over the barrier beaches. In areas where the coastline is low-lying and lagoons do not occur, the coast consists of rocky capes and points separated by narrow stretches of sand and pebble beach. Here tundra and fell-field often reach to the edge of the sea.

About 75 miles of the island's coastline consists of sea cliffs. The two major cliff areas are along the north shore of the island between Kangee and Cape Kitnik, and along the southwest coast from Booshu Camp to Powooiluk. The north shore cliffs seldom rise to more than 200 feet; they are formed by the action of the sea on stratified beds of soft volcanic rock. These cliffs often rise nearly vertically or are even sharply undercut, and may extend for several miles as an unbroken barrier. Erosion is rapid and great chunks of rock fall from the cliff faces during the spring thaw or after heavy rainstorms. As perilous as they may be, their rocky ledges provide nesting sites for hundred of thousands of sea birds. An isolated

FIG. 2. Map of St. Lawrence Island. Dots show locations where intensive collections were made by author. Open circles show areas visited and where some specimens were collected. Since many of the collections were made between points, not all collection locations are shown.

section of these cliffs form Stolbi Rocks, a group of vertical stacks which rise from the sea about three miles offshore from Cape Kitnik. Their sides are a sheer rise to a height of perhaps 250 feet. The thousands of breeding birds on this inaccessible islet effectively eliminate any vegetation of vascular plants.

The granite cliffs along the southwest coast of the island are of an entirely different aspect. The cliff faces are usually broken by cirques and talus slopes, so that unbroken sheer cliff faces stretching more than a mile or so are rare. In some cases the cliffs may rise to a height of 1000 feet. With their turreted peaks and castellated monoliths of gray granite, they remind one of a monstrous ruined city. This little visited area undoubtedly has the most spectacular scenery on St. Lawrence Island. While true sea cliffs are not found in areas other than the two mentioned above, steep talus slopes reach the coast at Gambell, Tapphook, and Southeast Cape.

Approximately one-half of the land area of St. Lawrence consists of lowlands with an elevation of less than 100 feet above sea level, a considerable fraction of which is covered by shallow lakes and ponds ranging in size from a few yards to a mile or more in diameter. These ponds are usually shallow, with low banks and ephemeral inlets and outlets. The surrounding tundra is poorly drained and often saturated with water, or even covered with standing water thoughout the growing season. There are several rivers of considerable size on the island. The lower reaches of the rivers are broad and sluggish, with winding channels and many cutoff lakes. This is particularly true of the Koozaata River in the south-central portion of the island. Some 15 species of plants, otherwise unknown on St. Lawrence, grow in and around this river. Many rivers

are navigable by skin boat for comparatively long distances, and it would probably be possible to cross the eastern end of the island by boat with only a few short portages. Other rivers are swift and clear, and often contain well-developed gravel bars, where many unusual species are found.

The mountains of the eastern and western ends of the island appear to be uplift mountains, and the exposed rock is mostly granitic. The entire southwestern portion of the island consists of a dissected upland about 200 square miles in area and reaching elevations of 1500 feet. The tops of the mountains are broad, rolling, rock deserts, which often drop away sharply to valley floors and to the sea. This area is the only part of St. Lawrence which shows evidence of having been glaciated at some earlier time. There are several spectacular cirques and some broad U-shaped valleys. The valley glaciers probably never coalesced to the point of forming even a local ice cap. Large patches of firn are found at several locations, and a relatively minor change in the climatic regime of the island could result in the formation of small glaciers within a relatively short period of time. The mountains of southwestern St. Lawrence extend to the north and east as rolling, rocky plateaus, usually with an altitude of less than 500 feet. The northward extension culminates at Sevuokuk Mountain on Northwest Cape, while the eastward extension ultimately disappears under the lava flows of the Kookooligit Range. A mountainous spur to the northeast reaches the coast at Tapphook.

Perhaps the most salient geographical feature of St. Lawrence is the Kookooligit Range, which is an oval shield of Pleistocene lava forming the central portion of the island. This shield is about 15 miles wide by 20 miles long. The range begins as a series of sea cliffs and escarpments and gradually rises to an altitude of 1500 feet at the center. Numerous cinder cones protrude from the shield, the highest of which rise to about 2200 feet, the highest point on the island. At least one large caldera and several smaller craters are present on the Kookooligit shield. They are filled with water, and often do not thaw until late July or in August. Although many of the lava flows have a very fresh appearance, no fumaroles, warm springs, or other indications of recent volcanic activity are to be found. The major lava flows apparently date from the early Pleistocene (Hopkins, *et al.* 1964). Streambeds around the periphery of the Kookooligit Range cut through the lava into earlier deposits, and petrified wood and coal are found in the streambeds. Petrified wood from St. Lawrence has been identified as *Metasequoia* (Chaney 1951). Isolated cinder cones are found along the entire northeastern portion of St. Lawrence, as far east as the Punuk Islands, which were at least partially formed by volcanic activity. These cones are probably related to the same volcanic episode which resulted in the formation of the Kookooligit Range. There are no indications of volcanic activity west of the western border of the Kookooligit Range. The major mountains of the eastern end of St. Lawrence are isolated block mountains, the most impressive of which is the rugged Kinnepaghulghat Range which rises to about 1800

feet and covers 40 square miles near Northeast Cape. The smaller Kialegak Range forms Southeast Cape, and Soomagat and Mygapowit Mountains lie in the isolated interior of the island.

The Bering Land Bridge and Refugium

Any study concerned with the history of the biota of St. Lawrence Island must take into account the history of the Bering Land Bridge. The history of the land bridge and its biogeographical implications have been covered in detail elsewhere (cf., Simpson 1940; Hopkins 1959a; Colinvaux 1964 and particularly Hopkins 1967) and need only be summarized here.

The floor of the northern part of the Bering Sea and of most parts of the Chuckchi Sea lies only 50 to 100 meters below present sea level. The sea floor is actually a continental shelf which, if emergent, would make Alaska and Siberia a continuous land mass (Fig. 1). The land bridge thus formed would be about 1000 miles wide and stretch from near the Pribilov Islands northward to the vicinity of Point Barrow, Wrangel Island and the New Siberian Islands. It has long been recognized (Simpson 1940) that the mammalian fauna of western North America and Asia showed strong evidence of interchange throughout most of the Tertiary. The obvious and generally accepted conclusion is that a broad land connection existed in the vicinity of the Bering Sea continually, if not continuously, throughout the Tertiary.

During the Pliocene, crustal warping in the Bering Sea region resulted in a lowering of the Bering-Chuckchi Platform (Hopkins *et al.* 1964) to approximately its present level, and the land connection was severed. However, during the major glacial advances of the Pleistocene, the level of the oceans throughout the world was lowered by as much as 100 meters, due to the vast amounts of water which were tied up in continental ice sheets. If it is assumed that the level of the Bering-Chuckchi Platform was more or less stable throughout the Pleistocene, the obvious implication is that, during each of the four or more major glacial advances, the Bering Land Bridge was reopened. The land bridge would have existed in the form of a vast level plain. The various islands, including St. Lawrence, would then have been isolated highlands and mountain ranges. For reasons that are not fully understood at present, most of central and western Alaska and eastern Siberia were never subjected to extensive glaciation during any of the Pleistocene glacial advances. Therefore, the Bering Land Bridge not only served as a corridor for the migration of plants and animals between Alaska and Siberia, but it also must have served as a great refugial area for many elements of the arctic biota which elsewhere were either exterminated or driven out by the advancing ice sheets (cf., Hultén 1937).

There can be little doubt that the climate of the land bridge during much of the Tertiary was of a more or less temperate nature. Petrified wood of tertiary age occurs on St. Lawrence, and many of the mam-

malian species which crossed the land bridge are considered to belong to groups adapted to temperate climates. The Pleistocene climate of the land bridge is less clear. Most workers (cf., Colinvaux 1964) believe that the climate of the land bridge, whenever it was open during the Pleistocene, was essentially arctic and probably no warmer than the present climate of the area. However, there are some anomalous data indicating that the situation may be more complex. For example, Colinvaux (1967) notes a number of genera of the Pleistocene pollen flora not presently on St. Lawrence Island, but which do occur in more southern parts of Alaska. The presence of large amounts of pollen of the *Umbelliferae* in a submarine core from near Kotzebue Sound (Colinvaux 1964) could indicate the presence of a rich umbelliferous tundra in that area at about the time when the land bridge was submerged for the last time. Tundra of this type is now seldom found north of the Pribilov Islands.

The treeless condition of arctic land areas seems to be caused largely by low amounts of available summer warmth, and low summer temperatures are normally associated with a maritime climate, making the treeless tundra a coastal phenomenon. Tundra areas do not exist at low elevations, even in the far north, more than about 200 miles from the nearest large body of water. During the existence of the land bridge, it is assumed that the emergent Bering-Chuckchi platform was at least 1000 miles wide, and it seems reasonable to conclude that the climate must have been highly continental at some periods, with relatively warm summers and cold winters. The presence of small glaciers on the Pribilov Islands (Hopkins & Einarsson 1966) and on St. Lawrence Island during the Pleistocene are considered evidence that the land bridge climate was colder than the present one. However, no conclusive dating is available for the times when these areas were glaciated and it is quite possible that these minor glaciations were out of phase with the major glacial periods. Small alpine glaciers are usually more dependent on an adequate supply of precipitation and cool summer temperatures than upon the yearly mean temperature, and it is doubtful that glaciers could form near sea level on St. Lawrence unless an extremely maritime climate prevailed. Therefore, it might be considered likely that the glaciers of the Bering Sea islands were formed at the beginning of glacial periods, before the land bridge had emerged and that they did not persist throughout land bridge times. Recent studies (McCulloch, *in* Hopkins 1967) indicate that at some time during the Pleistocene the timberline was considerably closer to the Pribilov Islands than it is at present, indicating that warmer conditions, at least with respect to summer temperatures, prevailed in Alaska during the Pleistocene than at present. In general, the evidence indicates that the Bering Land Bridge, during the Pleistocene, was a broad and probably treeless plain, and that a more or less arctic climate prevailed. From present knowledge, it does not seem justified to conclude that the climate of the land bridge was colder than at present, and

there is certainly some evidence that summers in parts of the land bridge may have been warmer than now.

Weather and Climate

The climate of St. Lawrence Island can be characterized as polar maritime, with short, cool summers and with a comparatively heavy precipitation for an arctic area. Due to the presence of the polar ice pack during the winter and spring, the warming influence of the surrounding sea is not strongly felt during the cold months, and winter temperatures are comparatively low.

Climatic data for Gambell and Savoonga are summarized in Fig. 3, including data from some other arctic areas for comparison. As both Gambell and Savoonga are located on the north coast of the island, these locations probably have a more extreme maritime climate than areas in the southern portion. Clear days are a rarity during the summer months at Gambell, but there are sometimes several in a row in the southern part of the Kookooligit Range, although at the same time Gambell Mountain may be blanketed in dense fog.

The comparatively low temperatures experienced during June in Savoonga are probably due to the pack ice remaining in the vicinity of Savoonga for a week or two longer than at Gambell. The strong ocean currents which sweep past the Gambell Peninsula apparently are effective in clearing the ice pack earlier there. The absolute maximum temperature recorded at Gambell is 65°F, and it is unusual for the daytime temperature to rise much above 50°F. Therefore, daytime temperatures at Gambell are quite comparable to those recorded along the arctic coast of Alaska and in the Canadian Arctic Archipelago. These temperatures are several degrees lower than those recorded on the mainland Bering Sea coast of Alaska. No climatic data have been gathered from southern coastal and interior portions of St. Lawrence, but clearer weather in these areas probably allows temperatures to rise to a slightly higher level than at Gambell. Conversely, increased radiational cooling in these areas can make them more prone to summer frosts, which almost never occur at Gambell. Winter temperatures on St. Lawrence are comparatively high for an arctic area. The mean January temperature at Gambell is 20°F higher than at Point Barrow, and short periods of thawing temperatures may occur at any time of the year.

Precipitation on St. Lawrence is unusually high for an arctic area. It is responsible for the extreme wetness of many of the tundra areas of the island, and also for the relatively large areas covered by permanent ice and snow. Snowfall is exceedingly variable, but it may reach as high as 190 inches. Most of the snow which falls on exposed areas is blown out onto the icepack, but large amounts are also deposited in cirques and ravines. Mean wind speed throughout the year at Gambell is 17.8 mph. Calm days are rare, and winds of gale force may rise suddenly at any time.

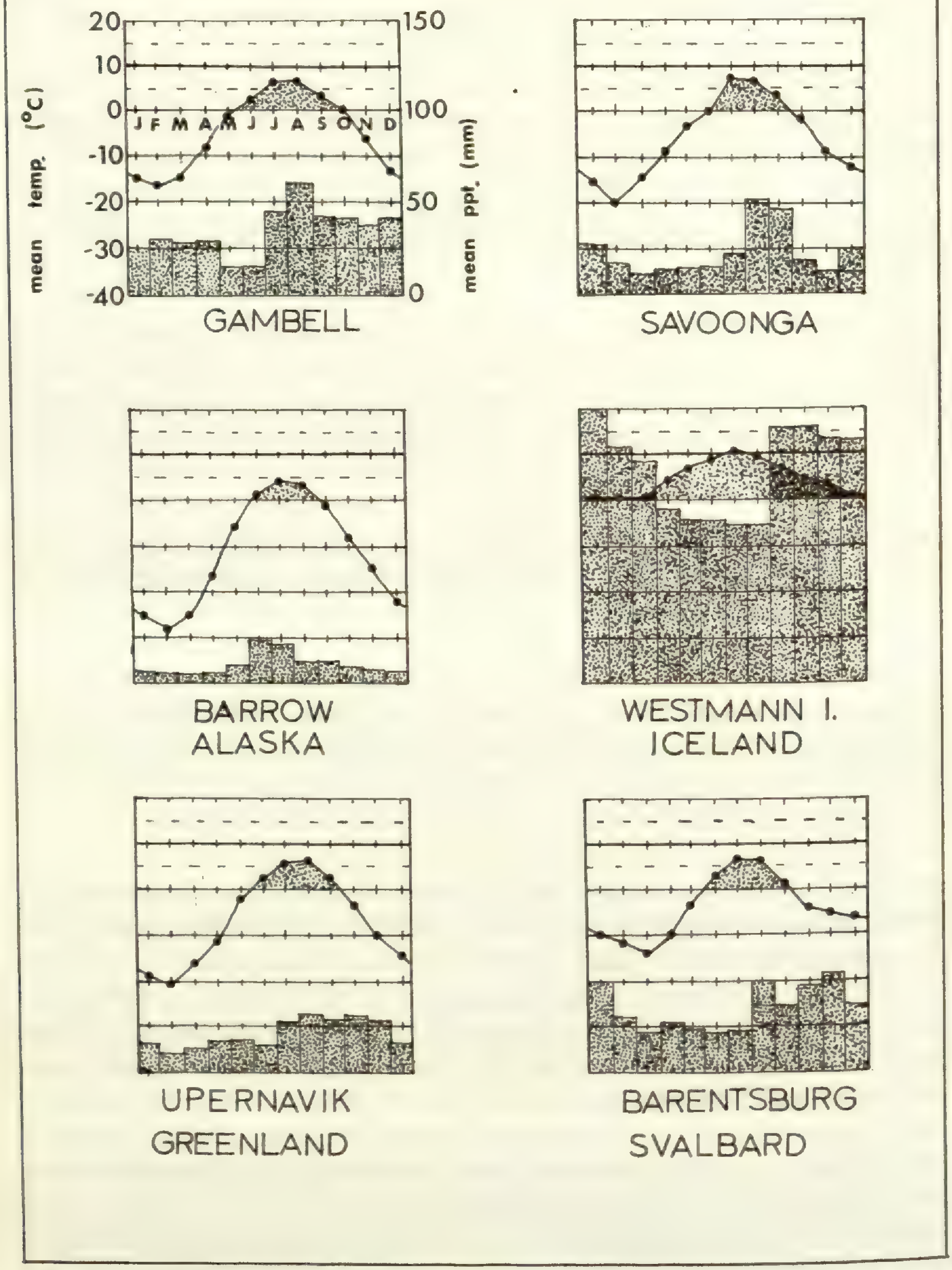


FIG. 3. Graphs showing mean temperature and precipitation by month for two stations on St. Lawrence Island, with similar data from other far northern stations for comparison.

During late summer and autumn, violent storms, usually from the southwest, may last for days or weeks at a time.

The growing season on St. Lawrence usually begins in early June when the snow begins to melt in exposed areas. By late June the willows are

in leaf, and most of the early tundra flowers, such as *Lloydia, Anemone, Ranunculus, Primula,* and *Pedicularis* are in bloom. Summer lasts through July and the first two or three weeks of August; by late August, most plants have completed their life cycles, and the leaves on willows and *Arctostaphylos* have begun to turn. Early September brings the first snow and freezing weather, and the ice pack begins to form in late October.

Permafrost, Frozen Ground Features and Soils

Permafrost. Perennially frozen ground underlies most of the land area of St. Lawrence Island. The only exceptions seem to be the beds of lakes with a depth of over four feet. This is undoubtedly because lakes on the island do not freeze to a depth of more than about four feet during the long but only moderately cold winters. The lack of permafrost beneath lakes probably has no correlation with the depth of permafrost in terrestrial locations. There are no data available on the depth to which permafrost extends on St. Lawrence.

The depth of the active (seasonally thawed) layer of the soil varies greatly depending largely on conditions of drainage and vegetation. The active layer is most shallow in wet tundra with a complete vegetation cover, particularly where *Sphagnum* is abundant and the depth of the thaw may be no more than six inches during the entire summer. In more mesic situations, the depth of thaw averages from two to three feet, with deeper thawing occurring along stream banks, on solifluction lobes and on raised hummocks. The depth of thaw of raised beaches, barrier beaches, etc. is not known. I found permafrost at a depth of about three feet in a raised beach near Gambell in early July, indicating that the total depth of thaw is considerably greater than three feet.

Frozen Ground Features. All of the soil features commonly associated with intense frost action (cf., Flint 1957) occur on St. Lawrence Island. Frozen ground features have a considerable and not entirely deleterious effect on the constitution of local vegetation. In particular, the minor relief afforded by raised features on patterned ground often allows the development of a comparatively complex vegetation in areas which otherwise would support only bog.

Patterned ground is found on all the low-lying areas of St. Lawrence Island, and also on many alpine and fell-field terrains. Where it is wet and low-lying, the commonest form of patterned ground is a system of low-centered polygons. The relief of these features is so slight that it is not readily visible from ground level, and the effect on the vegetation is correspondingly small. In other areas, high-centered polygons may rise to two or three feet above the surroundings. Their effect on the vegetation is considerable, and there are a number of species that are essentially confined to these areas. On flat alpine areas and fell-fields, patterned ground usually occurs in the form of sorted stone rings. With increasing slope, the rings are distorted into ovals and ultimately into parallel strips.

These features are usually associated with highly unstable soil and intense frost heaving, and the poor vegetation of these areas reflects this.

Frost boils are of common occurrence on wet tundra. They are found by the entrapment of semiliquid clay between the permafrost and a contracting layer of frozen soil on the surface. Ultimately, the frozen surface cracks open, and the clay spreads out over the surrounding vegetation, usually destroying it. Frost boils are revegetated slowly, and they are often visible for many years after their formation.

Solifluction is common where there is some slope and a fairly thick mantle of soil or gravel. Solifluction tends to concentrate soil at the edges of advancing solifluction lobes which are raised somewhat above the surrounding terrain, with the result that they are comparatively well drained and deeply thawed during the summer. The edges of these lobes often support a comparatively lush vegetation, and there are some species which are more or less restricted to such areas, at least on St. Lawrence Island.

Soils. To my knowledge, no work has been done on the soils of the island. However, similar soils on the Arctic Slope of Alaska have been studied intensively (Tedrow & Cantlon 1958; Drew & Tedrow 1962). Tedrow and Cantlon (*loc. cit.*) distinguish a single zonal soil in arctic areas designated as arctic brown soil. It is a product of podsolization, and develops only under conditions of adequate drainage, a deep active layer, and moderate soil particle size. As a consequence, this type of soil is seldom developed over large areas. On St. Lawrence, arctic brown soil is found along stream banks, on solifluction lobes and particularly on the stabilized backshores of barrier beaches. The total area involved is probably less than 5 per cent of the land area of the island.

With increasing wetness, arctic brown soils grade into tundra and ultimately bog soil. This is the most important soil type on St. Lawrence Island and probably covers over half the island's land area. With decreasing depth of bedrock, arctic brown soil grades into a lithosol, while with increasing particle size it grades into a regosol. The distinction between these two types is often not clear, as in the case of a slope or plateau mantled with frost-riven rock fragments. In any case, "soils" of these types are of major importance on St. Lawrence Island, covering most of the mountainous areas, fell-fields, and many of the less stable beach ridges. On a local level, variation in the nature of soil is often closely correlated with various types of patterned ground, and it has been proposed that arctic soils should be classified on the basis of both the genetic soil profile and the patterned ground (Drew & Tedrow 1962).

It is axiomatic that the type of soil is closely correlated with vegetation. Bog soil usually supports a closed community consisting of a few species of grasses and sedges, while arctic brown soils commonly support a more complex community of many species of plants. Other soil types usually support a poorly developed vegetation, although the *Elymus* zone on the foreshores of beaches is an exception to this rule.

Vegetation and Habitats

The vegetation of St. Lawrence Island consists entirely of a low, generally herbaceous growth which ranges from essentially complete cover in some wet areas to virtually no cover, at least of vascular plants, on alpine rock deserts and lava flows. However, lichens, particularly species of *Cladonia* and *Cetraria,* are often common in these areas. Tussock forming species, of which *Eriophorum vaginatum* is the most important, are rare or absent on St. Lawrence. Tussock tundra does not occur on the island, although it is often well-developed on the mainland of northern and western Alaska. Shrubby species are also of little importance in the St. Lawrence Island vegetation. The only common shrub willow is *Salix pulchra,* and this species normally does not exceed one foot in height, although in riparian gravel plants may be two feet or more tall. There are reportedly some areas on the southern slopes of the mountains on the eastern end of the island which support shrubby growth. I have not been able to find these areas and cannot comment on the species involved.

A reasonable breakdown of the habitats on the island would distinguish four major types, each with a corresponding vegetation formation. The types are: bog and wet tundra; alpine and fell-field; mesic tundra; and aquatic habitats. The first two types are, in terms of area, by far the most important. There is a strong correlation between the major habitats and the soil types discussed in the previous section. A number of minor habitats are also distinguishable on St. Lawrence Island. Generally, these result from the action of man or other biotic factors.

Wet Tundra. Wet tundra is, in terms of area covered, the most important vegetation formation of St. Lawrence Island. It covers approximately half of the land area of the island. Wet tundra is most commonly developed at low altitudes, and it is most prevalent on the level plains of the eastern end of the island. However, small patches of typical wet tundra occur in alpine areas wherever there is impeded drainage. On many of the rolling plateaus there is not enough relief to provide adequate drainage, and here also wet tundra is dominant. The vegetation cover on wet tundra is usually close to 100 per cent. Exceptions occur in areas where frost boils are abundant or where intense frost action disturbs the vegetation.

In the wettest tundra, *Carex aquatilis* is the most abundant species, and may form nearly pure stands over large areas. In better drained areas, *Eriophorum angustifolium* becomes dominant, with *Dupontia Fischeri* also often being of major importance. Wet tundra areas are usually dotted with *Sphagnum* hummocks, frost boils and raised polygons. The relief of these features is often enough to have a considerable effect on drainage, with the result that many wet tundra species are found only in these places. The species most commonly found on hummocks include: *Salix arctica, S. pulchra, Rumex arcticus, Saxifraga heiracifolia, S. punctata, S.*

nudicaulis, Rubus chamaemorus, Vaccinium vitis-idaea, Senecio atropurpureus and *Petasites frigidus.*

Alpine Areas and Fell-fields. The term alpine as used here does not denote any particular amount of elevation, as typical alpine habitats extend down to sea level on many parts of the island. There is no clear-cut distinction between alpine areas and fell-fields, but the latter term is generally used for areas of unconsolidated rock and gravel, whether they occur on mountains or not. Sizable areas in the interior of St. Lawrence Island are flat and often raised only a few feet above the surrounding wet tundra, but nevertheless have developed a typical open fell-field vegetation containing essentially the same species as those found in the higher mountains.

Alpine and fell-field vegetation is developed on 30 to 40 per cent of the land surface of St. Lawrence. It ranges from less than 50 per cent cover on unconsolidated gravel and rock to no cover on lava flows and rock deserts at high elevations. In general, conditions in alpine and fell-field areas are rather dry, but the impermeability of the substrate allows water to be trapped in many small pockets and seepage areas, even at higher elevations. A few species, e.g., *Ranunculus glacialis, Claytonia acutifolia* and *Polygonum bistorta,* are usually confined to these areas. Some gravel flats at low elevations also may be damp, or even saturated with water. There, frost action is often extremely intense and the thin vegetation cover probably is due to soil instability. One can often find sizable clumps of vegetation which have been uprooted and overturned by frost action on wet gravel flats.

Rock deserts are found in the mountain ranges on the eastern and western ends of the island, particularly at the higher elevations of the Poovoot Range near Boxer Bay. The substrate here consists of rather large fragments of frost-riven granite. Soil is found only in small pockets where the mantle of broken rock is thinnest, and over large areas there may be no significant growth of vascular plants. However, lichens of several genera are often abundant on the surface of the rocks.

Lava flows occur in the central and southern portions of the Kookooligit Range. The lava here is relatively unweathered, and usually supports a weakly developed vegetation, similar to that found on other rock deserts. In the northern part of the Kookooligit Range, the lava is softer, more deeply weathered, and is often cut by deep stream banks. A number of species are characteristic of these areas, and some of them are not found elsewhere on the island. Examples are: *Saxifraga flagellaris, Chrysosplenium Wrightii* and *Phyllodoce coerulea.* The first two species are probably calciphiles.

The alpine habitats of St. Lawrence are so varied that it is difficult to characterize them in terms of the species present in the plant communities. The following species commonly occur on the wetter alpine habitats, and they are often abundant: *Lycopodium selago, Deschampsia*

caespitosa, Juncus biglumis, Luzula confusa, Salix phlebophylla, S. polaris, Oxyria digyna, Saxifraga punctata, Sedum rosea, Cassiope tetragona, Primula tschuktschorum and *Artemisia arctica.* In drier areas, species such as *Hierachloe alpina, Trisetum spicatum, Arctagrostis latifolia, Carex nesophila, Arenaria arctica, Potentilla* ssp., *Oxytropis nigrescens, Pedicularis lanata* and several species of *Artemisia* are often common.

Mesic Tundra. The term mesic tundra as used here is something of a catchall phrase, since it includes a number of superficially unrelated habitats such as sandy backshores, riparian gravel situations and upland tundra. However, in all of these habitats the active layer of the soil is comparatively deep and a zonal soil (arctic brown soil) has been developed. The area covered by mesic tundra on St. Lawrence Island is comparatively small, perhaps 5-10 percent of the total land area of the island. Except along the coast, mesic tundra is confined to areas in the central and particularly the south-central portion. In other areas it is usually confined to small patches on solifluction lobes, along streambanks and on raised beaches.

Floristically, mesic tundra is the richest habitat on the island. Perhaps 90 per cent of the non-aquatic flora of the island can be collected on mesic tundra, and the majority of the rarer terrestrial species are found only in these areas. Examples are: *Veratrum album, Ranunculus Turneri, Gentiana auriculata* and *Campanula uniflora.* A number of other species are common to abundant on mesic tundra, but are practically unknown on the rest of the island. Among these are: *Calamagrostis canadensis* ssp. *Langsdorffii, Juncus castaneus, Potentilla palustris, Rubus arcticus* and *Epilobium anagallidifolium,* all of which grow on mesic tundra in interior portions of the island. Such species as *Aconitum delphinifolium, Primula borealis, Pedicularis verticillata, Chrysanthemum arcticum* and *Artemisia Tilesii* are often abundant on backshores but rare elsewhere. *Salix Chamissonis, Silene acaulis, Wilhelmsia physodes, Epilobium latifolium* and *Pedicularis Oederi* are confined to riparian gravel situations.

A characteristic type of mesic tundra is developed on the foreshores and backshore areas of the 200 or more miles of barrier beach surrounding the island. In many areas, the lagoons behind these beaches have been reduced to little more than ephemeral ponds and puddles, and the backshore may be a mile or more wide. The flora found on backshore and foreshore areas on the periphery of the island is quite uniform. The foreshore communities reach from the level of the highest storm tides to a point somewhat behind the greatest elevation of the barrier beach. As the beaches are normally rather steep on the seaward side and slope away gradually to the landward, the foreshore community normally covers a much smaller area than does the backshore community. The foreshore community is always dominated by a thick growth of *Elymus arenarius.* Between the sea and the *Elymus* zone is often a narrow zone in which *Honckenya peploides, Mertensia maritima* and *Senecio pseudo-arnica*

are common; higher up the beach *Conioselinum chinense, Angelica lucida* and *Lathyrus japonicus* may be mixed with the *Elymus*, but none of these species is common. The backshore community is neither as lush nor as thick as that of the foreshore, but it is much more complex, and as many as 75 species may be found on an area of backshore of no more than a few acres. Among the more common species are: *Equisetum arvense, Festuca brachyphylla, Phippsia algida, Luzula tundricola, Salix reticulata, S. ovalifolia, Cerastium Beeringianum, Sagina intermedia, Melandrium apetalum, Polemonium boreale, Pedicularis verticillata, Artemisia Tilesii, A. arctica* and *Chrysanthemum arcticum.* The floristic richness of the backshore zone is due to its generalized habitat in which alpine species such as *Papaver radicatum, Saxifraga flagellaris* and *Androsace ochotensis* may be found within a few feet of aquatic species such as *Hippuris vulgaris* and *Ranunculus Pallasii.*

Aquatic Habitats. Although a large proportion of the land area of St. Lawrence is covered by fresh water lakes and ponds, the aquatic flora is usually poorly developed, and many of the tundra ponds contain no true aquatic plants. The shallow edges of the ponds usually support a dense growth of semi-aquatic species such as *Arctophila fulva, Eriophorum angustifolium* and *Carex aquatilis*, while the deeper areas may be devoid of vascular plant life. A few species of true aquatics are widely distributed over the entire island; among these are *Ranunculus hyperboreus, R. Pallasii, Potentilla palustris* and *Hippuris vulgaris*. In a small area in the south central portion of the island, a true aquatic flora is developed and ten or more species of aquatic plants are found there which are otherwise unknown on the island. Many are low arctic species and make up the major proportion of the low arctic elements of the St. Lawrence flora.

Minor Habitats. Several habitat types which do not fit into the major divisions discussed above occur on St. Lawrence. Many appear to be dependent on large quantities of nitrogen introduced into the soil by the activities of man and other animals. Bird cliffs are found along much of the more rugged coastline of the island. In areas where nesting activity is most intense, the soils consist almost entirely of the droppings of sea birds and the plant community consists of the nitrophiles *Phippsia algida* and *Cochlearia officinalis*. On the peripheries of the main breeding areas, other nitrogen tolerant species such as *Claytonia sarmentosa, Saxifraga rivularis, S. punctata* and *Sedum rosea* are common.

Human habitation sites. During the thousands of years that man has inhabited St. Lawrence, large amounts of refuse from human habitations have been deposited. The most extreme examples of this are found in some of the ancient village sites, such as Kialegak, Kookoolik and Sevuokuk where refuse mounds of several acres are found. They consist mainly of animal matter, particularly the bones of whale and walrus. Because of the cold climate, the nitrogen is released extremely slowly and human burial sites which are 500 to 1000 years old (H. G. Bandi, personal

communication, July 1967) are still visible as areas of slightly more luxuriant plant growth. When undisturbed, ancient village mounds have a vegetation quite similar to that of mesic tundra, because of good drainage. Growth is unusually rank, however, and a few species such as *Pedicularis verticillata* and *Artemisia Tilesii* predominate.

Ancient village sites which lie close to modern villages are usually honeycombed with pits, dug by the natives in search of artifacts. Because of the underlying permafrost, these pits are often damp or even filled with water and their sides support a lush growth of *Montia fontana, Koenigia islandica, Stellaria humifusa* and *Cochlearia officinalis.* The entire coast of St. Lawrence is dotted with the remains of single dwellings which can be seen for miles because boat racks, made from the jawbones of right or bowhead whales are often still standing. These individual sites are only a few square yards, but they support a flora which is the same as that of the larger village sites.

Animal burrows. Many gravelly areas have been extensively tunneled by arctic foxes (*Alopex lagopus*) and arctic ground squirrels (*Citellus parryi*). Tunneled areas usually support a dense growth of *Arctagrostis latifolia,* a species which otherwise seldom occurs in pure stands.

Waterfowl resting areas. Large flocks of migrating and molting waterfowl, mostly emperor geese (*Philacte canagica*) and snow geese (*Chen hyperborea*), congregate each year on certain parts of the island. The most favored points are at the extreme ends of large lagoons or near small ponds on the backshores near them. The soil in these areas is considerably enriched, and the grazing of the geese probably has some effect on the vegetation. The most common species in these areas are *Carex glareosa, C. rariflora* and *C. subspathacea.* On the bottoms of the shallow, ephemeral pools found in these areas, the same species as those occurring in pits of old village sites are usually abundant. Some pools may also support a dense growth of *Callitriche verna.*

Reindeer carcasses. At one time St. Lawrence supported an introduced population of reindeer which has been estimated to have contained up to 10,000 animals and reindeer herding was an important native industry. Apparently the herd grew too large for the carrying capacity of the range and in the late 1940's nearly all the herd died off, leaving carcasses strewn over the entire island. Fay and Cade (1959) mention that the vegetation in the vicinity of the carcasses was considerably more lush than in surrounding areas, but by 1966 this phenomenon had disappeared, although it is still possible to find reindeer skeletons on the tundra. It has been claimed that the poor vegetation of St. Lawrence is the result of overgrazing by reindeer, but this seems highly improbable. The major food of the reindeer presently found on the island is lichens, and the herd is usually found in the high barrens of the Kookooligit Range, where few vascular plants grow, but where a relatively rich lichen flora has developed. The absence of shrub and tussock tundra on St. Lawrence

seems to be correlated with the almost complete absence of tussock- and shrub-tundra forming species. The small reindeer herd which is now present on St. Lawrence probably numbers less than 500 animals and it seems to have no noticeable effect on the vegetation. It is almost inconceivable that reindeer have selectively eliminated any species from the island.

Construction. Three airstrips and several small U.S. Government installations, most of which are now abandoned, have been constructed on St. Lawrence during the last few years. Construction has been on such a small scale that it has had little effect on the vegetation of the island. The major effect has been produced by the mining of gravel for the airstrips, resulting in the formation of several shallow ponds in the neighborhood of Gambell and Northeast Cape. Organic matter has not yet built up in these ponds and the typical wet tundra species are for the most part absent. Instead, such species as *Calamagrostis deschampsioides, Festusca brachyphylla* and *Stellaria humifusa* are found growing semi-immersed in the ponds. The habitats of certain areas also have been disrupted by the passage of tracked vehicles. For example, the pebble beach behind Gambell was once covered by a thin, dry tundra, according to the older natives, but the area is now mostly sterile and supports only a few spears of *Elymus arenarius.*

Riparian gravel situations. Some of the large rivers on the island have developed gravel bars of some size. Where they are raised to such an elevation that they are seldom inundated, a typical mesic tundra formation develops, but where they are flooded, a community consisting mainly of *Salix pulchra* and *Epilobium latifolium* has developed. At a slightly higher level are found, in addition to the above species, *Wilhelmsia physodes, Parnassia Kotzebuei* and *Silene acaulis,* all of which are rare in other habitats.

Snow patches. Since the permanent snow patches on St. Lawrence Island contract steadily until early September, bare soil is constantly being exposed during the summer. A few species which can complete their life cycles in a short period of time can be found flowering at the edges of snow patches in late August. The commonest of these are *Chrysosplenium tetrandrum, Saxifraga rivularis, S. punctata* and *Primula tschuktschorum.*

History of Botanical Collecting

Although the Billings expedition of 1791, including the naturalists Carl Merck and John Main, made a landing on St. Lawrence, the first botanical collecting of any consequence was done by A. L. von Chamisso and J. F. von Eschscholtz of the Kotzebue expedition of 1816–17. They landed at a village near Southeast Cape (undoubtedly Kialegak, which must have been occupied at that time) on July 27, 1816 and again on July 10, 1817. Specimens of perhaps 60 species of vascular plants were collected, including the type specimens of *Eriophorum callitrix* and *Cardamine*

purpurea. Many of the specimens from this expedition appear to be lost, and there are few specimens collected by Chamisso and Eschscholtz in U.S. herbaria. However, a detailed list of specimens collected was published (Chamisso & Schlechtendal, 1826–1836).

Saint Lawrence was apparently not visited again by a botanist until 1879 when F. R. Kjellman of the Nordenskjold *Vega* expedition spent from July 31 to August 2 at some area on the northwest coast of the island. The exact location of the *Vega's* landing is not known, but Kjellman's plant list indicates that he did not collect in any of the higher alpine regions, and it seems likely that the landing was made in the vicinity of Northwest Cape. Several species (e.g., *Pyrola grandiflora, Andromeda polifolia* and *Linnea borealis*) included in Kjellman's collections are now rare or absent in the northwestern portion of the island. The results of his work on St. Lawrence were published in the form of a flora of the island (Kjellman 1882) in which 113 species, including those collected by Chamisso and Eschscholtz and by Kjellman himself are listed. He was particularly impressed by the strongly arctic vegetation. His observations indicate that it was markedly different from that of adjacent mainland areas even before the introduction of reindeer to the island.

In 1881, the steamer *Corwin,* in search of the DeLong expedition, landed on St. Lawrence on May 28, June 8, and July 4 with the naturalist John Muir aboard. The landing was made somewhere on the northwest coast. Muir, too, was impressed with the bleak and barren aspect of the island. He writes (Muir 1918):

> Saint Lawrence Island, as far as our observations extended, is mostly a dreary mass of granite and lava of various forms and colors, roughened with volcanic cones, covered with snow, and rigidly bound in ocean ice for half the year.

Muir's collections, now in the Gray Herbarium, contain few specimens from St. Lawrence. He (1918) mentions that *Silene acaulis, Andromeda, Ledum, Linnaea* and "several species of *Vaccinium*" were common. These are all rather rare on the island at present. Only two species of *Vaccinium* are known to occur there, one of which, *V. uliginosum,* is known only from a couple of isolated localities.

On July 13, 1899, F. V. Coville and T. H. Kearney of the Harriman Alaska Expedition landed at Northeast Cape, apparently for one day only. Their small collections, now at the U.S. National Herbarium, contain a few species which were previously unreported from the island.

In the summer of 1931, H. L. Mason visited Savoonga on June 26 and July 9, and collected at Aivichtook Lagoon on July 10 and the Naskok Lagoon on July 12. The main collection is at the California Academy of Sciences, with a number of duplicates at the Gray Herbarium. During the summer of 1931 and several succeeding summers, Otto William Geist made ethnographical and archaeological studies on the island. Geist traveled widely around the island by boat and apparently he was the first

white man to travel extensively on the south side of the island. Geist's collection of plants, mostly made during the summer of 1933, are located in Stockholm, the Gray Herbarium and the University of Alaska Herbarium.

Jacob Peter Anderson, the indefatigable collector of the Alaskan flora, spent September 3, 1938 at Savoonga and the following day at Gambell. The numbers of the specimens supposedly collected by Anderson on St. Lawrence are not all consecutive, indicating that there may be some confusion in the labeling. This would explain the fact that Anderson's supposed St. Lawrence collection, made during only two days, and in areas which the author has visited repeatedly, contains several species which are otherwise unknown from the island. Anderson's collections are in the Iowa State University Herbarium, with many duplicates in Stockholm, the Gray Herbarium and the University of Alaska Herbarium.

Hultén (1940) lists several other small collections from St. Lawrence. Among these are: E. O. Campbell in 1903; L. J. Palmer in 1921; and K. L. Chambers in 1938. He (1941–1950) also lists a number of specimens collected by George Haley, supposedly on St. Lawrence Island. In his list of botanical collections from Alaska, Hultén (1940) makes no mention that Haley ever visited St. Lawrence, and he also notes (Hultén 1946) that the labels of Haley's collections are not always reliable as to location. Several of the species supposedly collected from the island by Haley have not been found by other workers. It seems probable that the specimens were obtained elsewhere, perhaps on the Pribilov Islands.

Between 1940 and 1966, when my own work on St. Lawrence began, a few small collections were made on the island. The most important of these were made over a period of several years by Dr. Robert Rausch and Dr. Francis H. Fay of the Arctic Health Research Laboratory at College, Alaska, who collected single specimens from several parts of the island. The more recent of these have been placed at my disposal. The older collections were identified by Dr. John H. Thomas of the Dudley Herbarium of Stanford University. Dr. Thomas kindly sent me a list of the species he had identified. Porsild (1965) mentions a single collection of *Primula tschuktschorum* made at Boxer Bay by Franz Sauer in 1960. I have no further information on this collection.

My own work on St. Lawrence Island took place during the summers of 1966–67. I spent a total of about five months there, during which time I collected 1100 sets of specimens. The major collection specimens locations are shown in Fig. 2, but many were collected on walking trips between the locations indicated on the map. The most intensive collecting was done in the Boxer Bay area, along the Koozaata River and in the Kookooligit Mountains in the vicinity of Savoonga. I was able to spend less times on the eastern end of the island and consequently did not visit all of the mountain ranges in the area. My collections include specimens of 235 species, of which about 60 have not been reported from the island before.

Annotated List of Species

General Notes. The following is a list of the species of vascular plants which are known to occur on, or have been reported from, St. Lawrence Island. The arrangement of the species follows that of Hultén (1968a). Species listed numerically and not enclosed in brackets are accepted as being members of the present St. Lawrence Island flora. Bracketed species have been reported in the literature as occurring on the island, but, for one reason or another, exclusion from the recorded flora seems warranted.

The relatively small number of specimens collected on St. Lawrence by earlier workers are scattered in herbaria throughout the world. At the outset of the present study, it was felt that the limited amount of time and money available were best spent in field work on the island, rather than in trying to assemble all earlier specimens. Therefore, it is possible that some of the species excluded from the flora are represented by specimens which I have not seen. However, the majority of the unsubstantiated reports seem to be based on specimens which are either incorrectly labeled as to collection location or which were misidentified.

The nomenclature used generally follows that of Hultén (1968a, 1968b). No attempt has been made to include synonymy except in the cases where a species is treated under a different name in other major works on the arctic flora, as for example Porsild (1964) and Tolmatchev (1960–1966). In order to reduce repetition, the author's name is listed only for the first specimen in a sequence of several specimens of the same species under the designation, specimens examined. All specimens listed without indication of their present location are deposited in the Gray Herbarium.

The overall distributions of the species in the St. Lawrence Island flora have been treated in more detail than is customary in a paper of this kind. Since the second section deals with factors affecting the distribution of arctic plants, it seemed important to include a fairly detailed picture of the distribution patterns of the St. Lawrence Island flora. The northern limit of the distributions of the species under discussion is characterized by a zone number ranging from 1 to 4. An explanation of the zones is given later in this paper, and a map of the zone boundaries is given on page 94. The ranges of most of the species treated here are shown on dot maps by Hultén (1958, 1962, 1968a), Tolmatchev (1960–1966) and Porsild (1964).

I have tended to be somewhat conservative in the taxonomic treatment of many of the species discussed below. In several cases, groups of specimens which many workers would place in two separate species are "lumped," as in the cases of *Saxifraga davurica, Rubus arcticus* and *Polemonium boreale*. In these cases, my field experience in western Alaska has led me to believe that all of the specimens of these groups belong to a single population, at least on St. Lawrence Island. In the case of *Rubus arcticus*, for example, it is possible to collect specimens which many

workers would regard as belonging to two separate species from the same clone.

LYCOPODIACEAE

1. Lycopodium selago L.

Common in most alpine situations. Occasional on backshores and hummocks of wet tundra. Although not all specimens from the island have the appressed leaves typical of ssp. *appressum,* field observations indicate that the contention of Hultén (1968a) that two subspecies of *L. selago* occur on St. Lawrence is not justified.

SPECIMENS EXAMINED: *Young* 55, Tapphook; *251,* Savoonga; *278,* Northeast Cape; 369, Kialegak; *497,* Siknik; *614,* Boxer Bay; *741,* Gambell. *Mason,* July 12, 1931, Naskok Lagoon. Several other reports. Range: circumpolar, arctic-alpine; also stations in the southern hemisphere. Northern limit: upper zone 2.

2. Lycopodium clavatum L.

Small, sterile clumps were found occasionally on rocky alpine areas. The specimens apparently belong to ssp. *monostachyon.* The presence of this species on St. Lawrence is probably due to the continuous arrival of spores from adjacent mainland areas such as the Chukchi Peninsula.

SPECIMENS EXAMINED: *Young* 53, Tapphook Mountain; *210,* Savoonga; 328, Northeast Cape; 555, Gaedtuk; *711,* Boxer Bay. No previous reports. Range: circumpolar, low arctic and temperate regions, with stations in the southern hemisphere. Northern limit: upper zone 4.

3. Lycopodium alpinum L.

Uncommon on raised beaches and along gravel stream banks. Not found in the higher alpine areas.

SPECIMENS EXAMINED: *Young* 97, Kookooliktook River; 265, Ataakas Camp; 327, Northeast Cape; 378, Kialegak; 550, Gaedtuk. No previous reports. Range: nearly circumpolar, but with gaps in Canada and Siberia. Northern limit: upper zone 4, reaching zone 3 in East and West Greenland.

EQUISETACEAE

4. Equisetum scirpoides Michx.

Two distinct populations of this species may occur on St. Lawrence. Large, robust clumps are occasionally found on rock deserts and lava fields, while smaller, more delicate individuals are found in grassy tundra, usually along small stream banks. Other than size, there are no morphological features which reliably distinguish between these two forms.

SPECIMENS EXAMINED: *Young 207,* Kookooligit Mountains; *451,* Kialegak; 577, Gaedtuk. No previous reports. Range: circumpolar, arctic and cool temperate regions. Northern limit: zone 3, reaching zone 2 in Northeast Land and Novaya Zemlya. (*Equisetum fluviatile* L. ampl. Ehrh.)

Hultén (1968a shows a station for this species on St. Lawrence. Specimens which I consider to be abnormal individuals of *E. arvense* can be mistaken for *E. fluviatile,* which I have not collected on St. Lawrence.

5. Equisetum palustre L.

Small, sterile specimens collected at a single station on a mudbank in a slough of the Koozaata River are best identified as this species.

SPECIMEN EXAMINED: *Young 1354,* Koozaata River. No previous reports. Range: nearly circumpolar, low arctic and temperate regions. Northern limit: northern zone 4, reaching zone 3 at Vaigatch Island.

6. Equisetum arvense L.

Rather common along the shores of lagoons and small lakes, and at the edges of frost boils and other disturbed areas on wet tundra. Sterile shoots are seldom more

than 5 cm tall and do not develop a central axis. Fertile shoots are only occasionally found.

SPECIMENS EXAMINED: *Young* 73, Tapphook; *215*, Savoonga; *427*, Kialegak; 575, Gaedtuk. *Mason 6086*, Savoonga. Several other reports. Range: circumpolar, arctic and temperate regions. Northern limit: conforms almost perfectly to the northern edge of zone 2.

POLYPODIACEAE

7. **Cystopteris fragilis** (L.) Bernh.

A single station was found on a talus slope on the west bank of the Boxer River, about four miles upriver from Boxer Bay. None of the specimens have mature sori, so it is impossible to tell whether they represent ssp. *Dickieana* or ssp. *fragilis*.

SPECIMENS EXAMINED: *Young 1311*, Boxer River. No previous reports. Range: circumpolar, arctic and temperate regions, also with stations in the southern hemisphere. Northern limit: zone 2.

8. **Dryopteris fragrans** (L.) Schott

Occasionally found in crevices in the barren lava fields along the southern edge of the Kookooligit Mountains. Some specimens are unusually delicate, with fronds less than 5 cm tall and with the rachis slender and nearly devoid of scales. These specimens probably represent an ecologically induced condition rather than a genetic race.

SPECIMENS EXAMINED: *Young 549, 1383*, near Gaedtuk. No previous reports. Range: arctic alpine, circumpolar but rare in Greenland and Europe. Northern limit: barely reaches the southern border of zone 2.

SPARGANIACEAE

9. **Sparganium hyperboreum** Laest.

Fertile specimens were found in a small pool on a bank of the Koozaata River about five miles upriver from Gaedtuk. A sterile specimen collected in a small pool near Kialegak is probably also this species.

SPECIMENS EXAMINED: *Young 454* (?), Kialegak; *1347*, Koozaata River. No previous reports. Range: circumpolar, mainly arctic. Northern limit: northern zone 4, reaches the lower edge of zone 3 in West Greenland and northern Alaska.

POTAMOGETONACEAE

10. **Potamogeton perfoliatus** L.

Found at a single station in the upper reaches of the Koozaata River, where it formed an extensive patch in about five feet of water. The specimens clearly belong to ssp. *Richardsonii*, a well defined American race which is occasionally treated as a separate species.

SPECIMENS EXAMINED: *Young 1342*, Koozaata River. No previous reports. Range: (*P. perfoliatus sensu lato*) circumpolar, low arctic and temperate regions. Northern limit: zone 4, reaching southern zone 3 near Scoresby Sound, East Greenland.

11. **Potamogeton subsibiricus** Hagstr. (*P. Porsildorum* Fern.)

Sterile specimens were found on the bottom of the Koozaata River near Gaedtuk and in several small pools nearby.

SPECIMENS EXAMINED: *Young 1341*, Gaedtuk. No previous reports. Range: three small, very disjunct areas: the lower Yenesei Basin, Alaska, and southern Hudson Bay. Northern limit: not clear.

12. **Potamogeton vaginatus** Turcz.

Common on the bottom of the Koozaata River near Gaedtuk; usually found in two to six feet of water.

SPECIMENS EXAMINED: *Young 1346*, Gaedtuk. No previous reports. Range: not completely known. Apparently more or less circumpolar in arctic and temperate regions. Northern limit: not clear.

JUNCAGINACEAE

13. **Triglochin palustris** L.

Sterile specimens were found at one station, on a mud bank in a slough of the Koozaata River. The single collection of *Equisetum palustre* was made at the same spot.

SPECIMENS EXAMINED: *Young 1348,* Koozaata River. No previous reports. Range: circumpolar, arctic and temperate regions, not extending north into arctic Siberia. Northern limit: does not conform well to any zone boundary; reaches zone 3 in Greenland.

GRAMINEAE

14. **Hierochloe alpina** (Sw.) Roem. & Schult.

Of scattered occurrence on most of the drier rocky and alpine areas.

SPECIMENS EXAMINED: *Young 54,* Tapphook; *208,* Savoonga; *372,* Kialegak; *566, 1340,* Gaedtuk. Several other reports. Range: circumpolar arctic-alpine. Northern limit: closely approximates the northern edge of zone 2.

15. **Hierochloe pauciflora** R. Br.

Rare in dry alpine areas.

SPECIMENS EXAMINED: *Young 226,* Savoonga; *301,* Northeast Cape. Also reported by Kjellman (1882). Range: arctic; nearly circumpolar, but not known from Greenland or northern Europe. Northern limit: closely approximates northern edge of zone 2 throughout its range.

16. **Alopecurus alpinus** Smith

Rather rare; most commonly found in cirques and on talus slopes in the southwestern portion of the island. Most specimens have long awns inserted near the base of the lemma. They can therefore be placed in ssp. *Stejnegeri.* This is a rather well-defined race of the Beringean area (Hultén, 1942), but it is less distinct on St. Lawrence than in more southern areas, and transitions between ssp. *Stejnegeri* and ssp. *alpinus* occur on the island.

SPECIMENS EXAMINED: *Young 628,* Boxer Bay; *1411,* near Southwest Cape. *Chamberlain 66. Anderson 5169. Geist,* 1933. Range: circumpolar, arctic. Northern limit: occurs throughout zone 1. Not treated by Hultén in *Circumpolar Plants* (1962). This is apparently an oversight, as the species has a typical and unbroken circumpolar range.

17. **Phippsia algida** (Soland.) R. Br.

A nitrophile, this species is abundant and often dominant on bird cliffs and on old village sites. Elsewhere it is uncommon and inconspicuous. The distinction between *P. algida* and the closely related *P. concinna* (Th. Fries) Lindeb. can hardly be made on specimens from St. Lawrence Island. Hultén (1950, 1968b) considers a single specimen (Kjellman, Aug. 1, 1879, *pro parte*) to be *P. concinna;* this is supposedly the only specimen from North America. According to Hultén (1950), *P. algida* normally has two stamens, glabrous or slightly pubescent lemmas, and the caryopsis is normally most expanded above the middle. *Phippsia concinna* has a single stamen, more pubescent lemmas, and the caryopsis is broader below the middle. Scholander (1934) notes that on Spitzbergen, *P. concinna* has an expanded inflorescence and is not a nitrophile. Saint Lawrence specimens most commonly have a single stamen, rather pubescent lemmas, and the caryopsis is usually most expanded below the middle. In many ways, they appear to be intermediate between *P. algida* and *P. concinna,* resembling *P. algida* in general appearance and habitat preference and *P. concinna* in respect to the characters mentioned above. Since there is no indication that two populations can be distinguished in *Phippsia* specimens from St. Lawrence, I refer all specimens to *P. algida.*

SPECIMENS EXAMINED: *Young 230, 231,* Savoonga; *350,* Northeast Cape; *689,* Boxer Bay; *735,* Gambell. Several other reports. Range: (of *P. algida*) circumpolar, arctic. Also known from two alpine stations in western U.S. Northern limit: found throughout zone 1.

(*Phippsia concinna*) See under *P. algida.*

18. **Arctagrostis latifolia** (R. Br.) Griseb.

Fairly common on drier habitats, particularly near the burrows of ground squirrels and arctic foxes. Occasional on backshores. Most mature specimens have the elongated, deeply pigmented anthers typical of var. *latifolia*. Occasional specimens with shorter, lighter colored anthers are probably immature. Some specimens from mesic tundra areas on the southern portion of the island are rather tall and have expanded panicles, as is typical of var. *arundinacea*. In other characters they conform to var. *latifolia*, and it does not seem to be possible to separate the material into two populations.

SPECIMENS EXAMINED: *Young 70, 120,* Tapphook; *228,* Savoonga; *317,* Northeast Cape; *446,* Kialegak; 532, Siknik; *679,* Boxer Bay; *792,* Gambell. Several other reports. Range: circumpolar, arctic. Northern limit: zone 1.

19. **Calamagrostis canadensis** (Michx.) Beauv.

Abundant on mesic tundra in the central and southern portions of St. Lawrence. Rare or absent elsewhere. Saint Lawrence specimens are high grown, with large, open panicles; they are referable to ssp. *Langsdorffii*.

SPECIMENS EXAMINED: *Young 712,* Boxer Bay; *1397,* Gaedtuk; *Anderson 5150; Geist,* 1933. Hultén (1942) also lists a specimen (*Geist,* 1933) as *C. canadensis* ssp. *Langsdorffii* X *C. nutkaensis;* I have not seen the specimen. Range: circumpolar, arctic and cool temperate regions. Northern limit: zone 4, reaching zone 3 on the arctic coast of the Chuckchi Peninsula.

20. **Calamagrostis deschampsioides** Trin.

Specimens which are best identified as this species were found growing semi-immersed along the sandy shores of small ponds near Gambell and Kialegak.

SPECIMENS EXAMINED: *Young 465,* Kialegak; *750, 752, 763, 794,* Gambell. Also reported by Hultén (1942). Range: this species is apparently rare. Its range is poorly known; it seems to be essentially circumpolar, but very disrupted. Northern limit: said to reach Wrangel Island (Hultén, 1962), a lower zone 2 area.

21. **Calamagrostis neglecta** (Ehrh.) Gaertn., Mey. & Schreb.

Uncommon; found in some alpine areas and also along sandy shores of small ponds. There is a considerable amount of morphological variation in the material listed below. Some specimens with open panicles and long awns might be considered to belong to *C. kolymaensis* Kom. (cf., Porsild, 1965). The genus *Calamagrostis* in the Beringean region is so complex and poorly known that it seems best to treat it conservatively until more work has been done.

SPECIMENS EXAMINED: *Young 171, 229,* Savoonga; *564,* Gaedtuk; *767, 795,* Gambell. No previous reports. Range: circumpolar, arctic and cool temperate regions. Northern limit: apparently lower zone 3.

22. **Deschampsia caespitosa** (L.) Beauv.

Fairly common on dry tundra and alpine areas over the entire island. *Deschampsia caespitosa sensu lato* is a large and very involved complex of wide distribution. Two quite distinct forms are found on St. Lawrence Island. The more common form is rather variable, but generally seems to fall into ssp. *orientalis* Hult. (*D. brevifolia* of Porsild (1964), *D. borealis* (Trautv.) Roshev. of Tolmatchev, 1964). In some coastal areas, a rather distinctive form with involute, bluish-green leaves and small spikelets is sometimes found. This has been described as *D. glauca* Hartm. and as *D. caespitosa* var. *glauca* (Hartm.) Sam. Variety *glauca* is not recognized as a separate species here, although further study may change its status. The entire complex is in great need of a detailed biosystematic study before a full clarification can be made.

SPECIMENS EXAMINED: *D. caespitosa* ssp. *orientalis: Young 186,* Kookooligit Mountains; *663, 665, 672, 694, 1414,* Boxer Bay; *746, 750x,* Gambell; *1341, 1375,* Gaedtuk. *Geist,* 1933, Southwest Cape. *D. caespitosa* var. *glauca: Young 252,* Savoonga; *481,* Siknik. *Geist,* 1933. Range: the *D. caespitosa* complex is a wide-ranging arctic-alpine group; similar species occur in the southern hemisphere. Northern limit: zone 1. The ranges of the various segregates of the complex are difficult to discuss, since there is so little agreement on the taxonomy of the group.

23. **Trisetum spicatum** (L.) Richt.

Fairly common in most habitats. All specimens from St. Lawrence are low-grown, have short, broad glumes, and contracted panicles. According to Hultén (1959) they belong to ssp. *spicatum,* the most arctic form of the *T. spicatum* complex.

SPECIMENS EXAMINED: *Young 119,* Tapphook; *229,* Savoonga; *413,* Kialegak; 537, Siknik; *580, 589,* Gaedtuk; *675,* Boxer Bay; *798,* Gambell. Several other reports. Range: circumpolar arctic and temperate regions. Probably also represented in the southern hemisphere. Northern limit: closely approximates the northern edge of zone 2 throughout its range.

24. **Poa arctica** R. Br.

Occasional on alpine areas, rare on backshores and hummocks of wet tundra. It is often difficult to separate *P. arctica, P. alpigena* and *P. malacantha* in St. Lawrence material, as there seems to be no general agreement as to what the key characters are that differentiate the three species. The key given by Wiggins and Thomas (1962) seems to separate specimens rather accurately into three natural groups, although the presence or absence of scabrosities on the panicle branches seems to be of little value in identifying St. Lawrence specimens. *Poa arctica* characteristically has narrow, usually involute leaves, and an open pyramidal inflorescence with capillary branches. The lower branches are often reflexed and somewhat torulose. The first glumes are usually narrow, lanceolate, and less than 3 mm long. The entire spikelet seldom exceeds 5 mm in length, except in the case of viviparous plants. The ligule tends to be somewhat lacerate, but this character is variable enough in specimens of all three of the above species found on St. Lawrence to be ruled out as a key character. In *P. alpigena* the leaves are usually flattened and about 2 mm broad, and the branches of the panicle are normally shorter and somewhat more ascending than in the case of *P. arctica.* The first glume is usually about 3 mm long and more or less lanceolate; the spikelet is usually somewhat longer and bears more florets than in *P. arctica. Poa malacantha* (*P. Komarovii* of many authors) is usually larger and more robust than either of the two species mentioned above. The leaves tend to be relatively broad and lax, and old leaf sheaths are persistent around the base of the rather thick culm. The first glume is usually about 5 mm long and tends to be rather broad. All St. Lawrence Island examples of *P. malacantha* which I have seen are viviparous. The presence and position of cobwebby hairs at the base of the lemma seems to be of little significance in the identification of St. Lawrence Island specimens of *Poa.*

SPECIMENS EXAMINED: *Young 232,* Savoonga; *794, 1453,* Gambell. *Geist,* 1933, Poovookpuk. Several other reports. Range: (as several poorly defined infraspecific taxa and apomictic groups) circumpolar, arctic-alpine. Northern limit: zone 1.

25. **Poa eminens** Presl

This species is usually found only in the *Elymus* zone on the foreshores of beaches. I did not collect it on St. Lawrence, nor have I seen any specimens from the island, but Hultén (1942) lists several collected by Geist and Anderson, and it cannot be doubted that the species occurs there.

SPECIMENS EXAMINED: none. Range: coasts of the Bering Sea and north Pacific Ocean, southern Hudson Bay and the Gulf of St. Lawrence. This highly disjunct range is nearly identical to that of *Senecio pseudo-arnica,* another strand plant. Northern limit: not clear, as the range is limited.

26. **Poa alpigena** (E. Fries) Lindm.

Rare in snow-flushes and other well-watered alpine situations. See *P. arctica.*

SPECIMENS EXAMINED: *Young 232x,* Savoonga; *646,* Boxer Bay. No previous reports. Range: circumpolar, arctic-alpine. Northern limit: zone 1.

27. **Poa malacantha** Kom. (*P. Komarovii* Roshev. of many authors)

Common on rocky alpine areas and on some old village sites. See *P. arctica.* On St. Lawrence this is the commonest member of the *P. arctica* group. All plants which I have seen are viviparous.

SPECIMENS EXAMINED: *Young 261,* Savoonga; *695,* Boxer Bay; *1434,* Gambell.

Geist, 1933, Poovookpuk. Range: Beringean endemic. Northern limit: not clear because of limited range, but ranges north to Point Barrow, a zone 2 area.

28. **Poa paucispicula** Scribn. & Merr. (*P. leptacoma* Trin. of some authors)

Rather common on dry tundra and lower alpine slopes. The distinction between this species and *P. leptocoma* is not clear.

SPECIMENS EXAMINED: *Young 117, 118*, Tapphook; *625, 1321*, Boxer Bay; *1456*, Gambell. Also reportedly collected by Geist, Anderson (Hultén, 1942). Range: mountainous regions of eastern Asia and western North America. Northern limit: not clear, but ranges north to Wrangel Island, a zone 2 area.

29. **Arctophila fulva** (Trin.) Anderss.

Common on the shores of backshore pools and tundra ponds.

SPECIMENS EXAMINED: *Young 448*, Kialegak; *593*, Boxer Bay; *1396*, Gaedtuk. Several other reports. Range: arctic; essentially circumpolar, but absent in most of Greenland and eastern arctic Canada. Northern limit: zone 2.

30. **Dupontia Fischeri** R. Br.

Common to abundant on wet tundra, where it is sometimes a major component of the wet tundra community. Some specimens are clearly ssp. *Fischeri*, while others approach ssp. *psilosantha*. The difference is not clear and may depend partly on the habitat and state of development of the plant. There is no reason to believe that there are two separate populations on the island.

SPECIMENS EXAMINED: *Young 342*, Northeast Cape; *522*, Siknik; *678, 728*, Boxer Bay; *783*, Gambell. *Geist*, 1933, Boxer Bay. Several other reports. Range: circumpolar, arctic. Northern limit: zone 1.

[*Puccinellia phryganodes* (Trin.) Scrib. & Merr.]

Reported by Kjellman as *Glyceria vilfoidea* (Anders.) Th. Fries. The species is not included in the flora of St. Lawrence Island by Hultén (1968a). I prefer to exclude *P. phryganodes* from the island's flora until a voucher specimen is found. The species is to be expected on St. Lawrence.

31. **Puccinellia Langeana** (Berl.) Sørens.

Common to abundant on some village sites and backshore areas. Apparently a nitrophile. Specimens from St. Lawrence apparently do not conform well with any of the subspecies described by Sørensen (1953) from the Greenland area.

SPECIMENS EXAMINED: *Young 1448*, Gambell. *Geist*, 1933, Boxer Bay. *Anderson 5149*, Savoonga. Range: arctic, very disrupted but probably essentially circumpolar. Northern limit: not clear, but reaches zone 2 at Point Barrow and Wrangel Island.

[*Puccinellia pumila* (Vasey) Hitchc.]

Hultén (1942) treated the specimens here considered under *P. Langeana* as *P. pumila*.

32. **Festuca brachyphylla** Schult.

Common on backshores, raised beaches, and alpine slopes.

SPECIMENS EXAMINED: *Young 133*, Tapphook; *538*, Siknik; *588, 1393*, Gaedtuk; *688*, Boxer Bay; *751*, Gambell. Several other reports. Range: circumpolar, arctic-alpine. Northern limit: northern zone 2, reaching zone 1 at Elif Ringnes Island.

(*Festuca rubra* L.)

Hultén (1942) reports that this species was collected at Savoonga by J. P. Anderson. The presence of this widely introduced lowland form of *F. rubra* was shown on a dot map by Hultén (1962). It seems probable that this species was adventive at Savoonga at the time of Anderson's visit, and that it has since disappeared.

33. **Festuca altaica** Trin.

A single collection from a rocky streambed in dry tundra seems best identified as this species, although the awns on the lemma arise from a lacerate apex which appears similar to that of some species of *Bromus*. In other characters, the specimens do not resemble any species of *Bromus* known to occur in Alaska.

SPECIMENS EXAMINED: *Young 1397*, Gaedtuk. No previous reports. Range: eastern Asia and western North America, with outlying stations in eastern Canada. Northern limit: zone 3.

34. **Elymus arenarius** L.

Abundant on foreshores of sandy beaches, where it is the dominant constituent of the vegetation. Small stations are occasionally found on rock outcrops some distance from the coast. It is possible that these latter specimens may belong to the taxon variously treated as *E. interior* Hult. or *E. mollis* ssp. *interior* (Hult.) Bowden. I have not had an opportunity to examine them critically. The *Elymus arenarius* complex is often split into several species (cf. Bowden, 1957, Tolmatchev, 1964). Most of the specimens from the shores of St. Lawrence can easily be placed in the taxon known as *E. arenarius* ssp. *mollis* or *E. mollis* Trin.

SPECIMENS EXAMINED: *Young 132*, Tapphook; *345*, Northeast Cape; *458*, Kialegak; *485*, Siknik; *671*, Boxer Bay; *729*, Gambell. Several other reports. Range: *Elymus arenarius sensu lato:* essentially circumpolar, but rare along the coast of Siberia. Northern limit: zone 3.

CYPERACEAE

35. **Eriophorum angustifolium** Honck.

Abundant in wet tundra and often the major constituent of such vegetation, except in the wettest situations, where it is replaced by *Carex aquatilis*. In spite of its abundance, it is often difficult to find fertile specimens of *E. angustifolium* on St. Lawrence. There is no general agreement on the taxonomy of the *E. angustifolium* complex. Although the peduncles of St. Lawrence Island spcimens are only faintly scabrous as a rule, in other respects they resemble typical specimens of ssp. *triste*, the high arctic form of *E. angustifolium*. Hultén (1968a) claims that ssp. *subarcticum* also occurs on the island, but I can find no evidence that more than one population of *E. angustifolium* is represented in the island's flora.

SPECIMENS EXAMINED: *Young 146, 150, 246*, Savoonga; *308*, Northeast Cape; *656, 680*, Boxer Bay; *740x, 782*, Gambell. Several other reports. Range: circumpolar, arctic alpine. Northern limit: conforms almost perfectly with the northern boundary of zone 2.

36. **Eriophorum callitrix** Cham.

Chamisso's type specimen of this species was collected on St. Lawrence Island (Hultén 1943), but the species was not collected there again until my own visit. It is rare on St. Lawrence, as it apparently is throughout its range, and it was found only at a few scattered stations along the edges of small rivulets and snow patches.

SPECIMENS EXAMINED: *Young 1401*, vicinity of Southwest Cape. Range: apparently nearly circumpolar, but with several gaps. Northern limit: northern zone 3.

37. **Eriophorum Scheuchzeri** Hoppe

Rare: found once on a sandy backshore, once in a patch of alpine wet tundra. The only previous report of this species on St. Lawrence is by Kjellman (1882); Hultén (1942) doubted this report, as the specimen could not be found.

SPECIMENS EXAMINED: *Young 492*, Siknik; *1373*, Gaedtuk. Range: circumpolar, arctic-alpine. Northern limit: northernmost zone 2, reaching zone 1 in Canada and New Siberian Islands.

38. **Eriophorum russeolum** E. Fries

All specimens of this species from St. Lawrence have white bristles. There is a good deal of variation in the material, and it is possible to distinguish both var. *albidum* and ssp. *rufescens* (*E. medium* Anders. of many authors). As there is no distinct line of demarcation between the two forms, I prefer to consider them under one species. *Eriophorum russeolum* is not common on St. Lawrence; it is found in patches of wet tundra in alpine areas.

SPECIMENS EXAMINED: var. *albidum: Young 57*, Tapphook; *158*, Savoonga; *311*, Northeast Cape; *605*, Boxer Bay; *1363*, Gaedtuk. Subspecies *rufescens: Young 147*, 247, Savoonga; *400, 447*, Kialegak. Several other reports. Range: not entirely clear

because of taxonomic difficulties. Apparently nearly circumpolar, but absent in Greenland. Arctic-alpine. Northern limit: reaches zone 2 in Siberia.

39. **Eriophorum vaginatum** L.

Rare on St. Lawrence Island. Found at a few scattered stations on dry tundra. This species dominates the tussock tundra which is so common on the mainland of arctic Alaska. The absence of tussock tundra on St. Lawrence is due to the rarity of *E. vaginatum*.

SPECIMENS EXAMINED: *Young 738*, Gambell; *1372*, Gaedtuk. No previous reports. Range: nearly circumpolar, but rare in Greenland. Arctic and cool temperate regions. Northern limit: northern zone 3, reaching southern zone 2 in a few areas.

40. **Kobresia simpliciuscula** (Wahlenb.) Mackenzie

Found once, on the shores of a small fresh water lagoon.

SPECIMENS EXAMINED: *Young 145*, Tapphook. No previous reports. Range: arctic-alpine. Essentially circumpolar, but fragmented in Eurasia. Northern limit: zone 3, with a few stations in zone 2.

[*Kobresia myosuroides* (Vill.) Fieri and Paol.]

Reportedly collected by Eschscholtz (Meinshausen, 1900). This species is easily confused with *Carex glareosa*, which is common on St. Lawrence. I have never collected *K. myosuroides* there and so prefer to exclude the species from the flora until its presence can be supported by a modern specimen.

41. **Carex Jacobi-peteri** Hult.

Found several times at the edges of small tundra pools on the south side of the island. These are apparently the first collections of this rather distinctive species outside the type locality at Cape Prince of Wales.

SPECIMENS EXAMINED: *Young 626, 1335*, Boxer Bay; *1428*, Ataakas Camp. No previous reports. Range: see above.

(*Carex scirpoidea* Michx.)

Reported from St. Lawrence by Holm (1907) with no specimens cited.

42. **Carex pyrenaica** Wahlenb.

Found once, growing in wet tundra on the western end of the island. Most specimens of this plant from the Beringean region are considered to belong to ssp. *micropoda*, sometimes considered a separate species. The specimens from St. Lawrence appear to be somewhat intermediate between ssp. *micropoda* and the nominate subspecies which is native to Europe. The florets are more loosely arranged on the spikes than in most Alaskan specimens, and the lower perigynia are somewhat reflexed. Occasional florets have three stigmas.

SPECIMENS EXAMINED: *Young 1417*, Booshu Camp. No previous reports. Range: broadly amphi-Beringean, reaching from Alaska and western U.S. to Japan. Also in the Pyrenees, Balkan, and Caucasus Mountains. The species reaches the Arctic only in the Bering Sea region.

(*Carex maritima* Gunn.)

Reportedly collected by Chamisso (Meinshausen, 1900), but this species has not been collected on St. Lawrence since then. There are no phytogeographical reasons why the species should not occur on St. Lawrence, but since no modern specimens exist it seems best to exclude the species from the island's flora.

43. **Carex Lachenalii** Schkuhr

Of scattered occurrence on drier upland tundra. *Carex Lachenalii* is closely related to *C. glareosa*, a species usually found on rocky sea shores and in salt marshes. On St. Lawrence Island, the two species apparently form hybrids. Specimens with narrow leaves and lax culms are here treated as *C. glareosa*, while broader leaved specimens with erect culms are treated as *C. Lachenalii*. There are, however, some intermediate specimens.

SPECIMENS EXAMINED: *Young 142*, Tapphook; *449*, Kialegak; *718*, Gambell; *1367*, Gaedtuk; *1400* Powooiluk; *1406*, Boxer Bay. *Geist*, 1933, Poovookpuk. Range: circumpolar, arctic-alpine. Northern limit: northern zone 3, reaching zone 2 at Wrangel I.

44. **Carex glareosa** Wahlenb.

Common on wet tundra near the sea, particularly in areas which are subject to heavy salt spray. This species is represented on St. Lawrence by two rather well-marked subspecies, ssp. *glareosa* and ssp. *pribilovensis*. Subspecies *pribilovensis* is distinguished by its broad leaves and elongated perigynia scales; it is apparently quite rare, and I have never collected it on the island. See *C. Lachenalii*.

SPECIMENS EXAMINED: ssp. *glareosa: Young* 259, Savoonga; *463*, Kialegak; *480*, Siknik; *525*, Gaedtuk; *635*, *670*, Boxer Bay. Several other reports. Subspecies *pribilovensis: Anderson 5175*, Gambell. Range: circumpolar, arctic. As in the case of many other strand plants, the range is somewhat fragmented, and the species is apparently rare along the arctic coast of Siberia. Northern limit: zone 3.

45. **Carex aquatilis** Wahlenb.

Abundant, usually the dominant species in the wettest tundra areas and along lakeshores. Also occasionally found on backshores. Although there is considerable variation in the material, all specimens from St. Lawrence are probably best placed in ssp. *stans* (Drej.) Hult., an arctic race which is often treated as a separate species. Small specimens from backshore areas sometimes resemble *C. subspathacea;* they can be distinguished from it because of the more abruptly tapered apex of the perigynia and the more deeply pigmented beak of *C. aquatilis*. A few St. Lawrence specimens of *C. aquatilis* have some tristigmatic florets; otherwise they appear to be normal.

SPECIMENS EXAMINED: *Young 130*, Tapphook; *161*, Savoonga; *309x*, *325*, Northeast Cape; *422*, *436*, Kialegak; *535*, Siknik; *597*, *628*, *681*, Boxer Bay; *739*, *740*, Gambell. Many other reports. Range: circumpolar, arctic-alpine and northern temperate regions. Subspecies *stans* is the arctic race. Northern limit: follows the northern edge of zone 2. Reaches zone 1 at Elif Ringnes Island in Canada.

46. **Carex subspathacea** Wormsk.

Rather rare along the edges of small lagoons and backshore pools. The species is inconspicuous and may be more common than the few collections would indicate.

SPECIMENS EXAMINED: *Young 168*, Savoonga; *493*, *525x*, Siknik. Also reported by Kjellman (1882). Range: circumpolar, arctic. Like other coastal species, apparently not known from large areas of the coast of arctic Siberia. Northern limit: zone 3, reaching the lower edge of zone 2 in some areas.

47. **Carex Ramenskii** Kom.

According to Hultén (1942), a specimen of Kjellman's from St. Lawrence belongs to this species, which is closely related to *C. subspathacea*. A single collection of mine seems best identified as *C. Ramenskii*. However, my specimens are unusually robust in growth habit, and the spikes are borne on long, capillary pedicels. The determination of these specimens must therefore be considered tentative, and it is possible that they represent an undescribed species.

SPECIMENS EXAMINED: *Young 1422*, Kookoolik. Range: coastal areas around the Bering, Chukchi, and Okhotsk Seas. Northern limit: not clear because of limited range. Reaches Point Barrow, in zone 2.

48. **Carex stylosa** C. A. Mey.

A single specimen was collected on a rocky stream bank near Gaedtuk.

SPECIMENS EXAMINED: *Young* 568, Gaedtuk. No previous reports. Range: amphi-Beringean, also occurs at James Bay, the Gulf of St. Lawrence, and southern Greenland. This range pattern is similar to that of several strand species such as *Poa eminens* and *Senecio pseudo-arnica*. Northern limit: not clear, reaches zone 3 in arctic Alaska and Siberia.

49. **Carex podocarpa** C. B. Clarke (*C. montanensis* Bailey)

Found at several small stations in rocky areas near Gaedtuk. When bearing mature spikes, this species is quite distinctive, but specimens collected early in the season are easily mistaken for *C. nesophila*.

SPECIMENS EXAMINED: *Young 571*, *581x*, *1374*, *1380*, Gaedtuk. Also reported by Hultén (1942), but not shown as occurring on the island in a later dot map (Hultén,

1968a). Range: broadly amphi-Beringean, occurring in the mountains of Eastern Siberia and western North America south to temperate regions. Northern limit: not clear, but reaches Wrangel Island, zone 2.

50. **Carex nesophila** Holm

Common on a wide variety of habitats, particularly the drier alpine and tundra situations. Often found at high elevations. There is considerable variation in the specimens from St. Lawrence. In some cases the perigynia are indistinctly bitentate at the beak, and in a few cases a single stem leaf is present. These specimens are difficult to identify by means of the keys of Mackenzie (1941) and Hultén (1942, 1968a), but in most characters they seem to fall well within the range of variation of *C. nesophila.*

SPECIMENS EXAMINED: *Young* 32, *125,* Tapphook; *188, 194, 209,* Savoonga; *281, 282,* Northeast Cape; *664, 1342, 1343,* Boxer Bay; *756, 759,* Gambell; *1416,* Booshu Camp; *1389,* Gaedtuk; *1424, 1426, 1429,* near Ataakas Camp; *1432,* Kookoolik. Reportedly collected by Eschscholtz (Kükenthal, 1909). Range: Beringean endemic.

51. **Carex rariflora** (Wahlenb.) J. E. Smith

Found once at the edge of a small tundra pool in wet coastal tundra.

SPECIMENS EXAMINED: *Young 1420,* Kookoolik. Also reportedly collected by R. Rausch and F. H. Fay (J. H. Thomas, personal communication, 1967). Range: circumpolar, arctic-alpine. Northern limit: zone 3.

52. **Carex livida** (Wahlenb.) Willd.

Two small stations for this species were found, both in wet tundra areas. The St. Lawrence Island specimens are unusually low-grown and stoloniferous. The pistillate scales are dark purple, with light green nerves. Similar specimens have been collected at Attu Island, and they probably represent a slightly differentiated Beringean race of *C. livida.* The discovery of this rather rare species on St. Lawrence Island extends the range by several hundred miles.

SPECIMENS EXAMINED: *Young 148,* Savoonga; *657, 661,* Boxer Bay. No previous reports. Range: more or less circumpolar, but extremely fragmented. The species is not usually found in arctic areas. and it is almost unknown in arctic and temperate Asia. Northern limit: aside from St. Lawrence Island, the few artic stations of this species are in zone 4.

53. **Carex misandra** R. Br.

Found in a few scattered stations in mesic tundra.

SPECIMENS EXAMINED: *Young 1308,* Gambell; *1403,* near Powooiluk. Also reported by Meinshausen (1900). Range: circumpolar, arctic with a few alpine stations. Northern limit: closely follows the northern edge of zone 2.

(*Carex rotundata* Wahlenb.)

Reportedly collected by Chamisso and Eschscholtz (Meinshausen, 1900). Excluded from the flora because of lack of recent reports.

54. **Carex saxatilis** L.

Fairly common on solifluction lobes, stream banks, and other mesic situations on the south and central portions of St. Lawrence. All specimens seem to belong to ssp. *laxa,* which is sometimes treated as a separate species, *C. physocarpa* Presl.

SPECIMENS EXAMINED: *Young 1475,* Gaedtuk; *1485,* Powooiluk. Also reported by Holm (1907). Range: circumpolar, arctic-alpine. Northern limit: northernmost zone 3, reaching zone 2 at a few stations.

55. **Carex membranacea** Hook.

Uncommon on mesic tundra in the southern and central portions of the island. *Carex membranacea* is often considered to be a race of *C. saxatilis.* On St. Lawrence. the two species occur in the same habitats with no evidence of intergradation, and there seems to be no basis to doubt their status as distinct species.

SPECIMENS EXAMINED: *Young 1331,* Boxer Bay; *1402, 1405,* near Powooiluk. No other reports in the literature, but Hultén (1968a) indicates a St. Lawrence Island collection of this species on a dot map. Range: easternmost Siberia and North American arctic, exclusive of Greenland. Northern Limit: northern zone 3.

JUNCACEAE

56. **Juncus castaneus** J. E. Smith

Abundant on mesic tundra in the central and southern portions of the island. Elsewhere rare and usually confined to specialized habitats such as old village mounds. Occasional specimens are found with little pigment in the inflorescence. Specimens of this type have been called var. *pallidus*. I doubt that they are of any taxonomic significance.

SPECIMENS EXAMINED: *Young 563*, Gaedtuk; *727*, Boxer Bay; *781*, Gambell. Also reportedly collected by Anderson (Hultén, 1942). Range: circumpolar, arctic-alpine. Northern limit: closely follows the northern edge of zone 3, with a zone 2 station in north Greenland.

57. **Juncus biglumis** L.

Inconspicuous, but apparently fairly common along the edges of tundra ponds, streams, and in some alpine areas, usually in snow patches or where there is seepage.

SPECIMENS EXAMINED: *Young 217*, Savoonga; *450*, Kialegak; *503*, Siknik; *806*, Gambell; *1376*, Gaedtuk. Also reported by Kjellman (1882). Range: circumpolar, arctic-alpine. Northern limit: found throughout zone 1.

58. **Juncus** sp.

A single group of *Juncus* specimens from the edge of a shallow lake at Boxer Bay cannot be identified as any species presently known to occur in Alaska. In each case, the inflorescence of these specimens consists of only two florets. The flower floret is sessile or nearly so, the upper one borne on a pedicel about 5 mm long. Each floret is 5 to 7 mm long and dark brown in color, and the inflorescence is subtended by a bract from 1.5 to 4 cm long. The total height of the flowering stem is less than 1 dm. Leaves are equitant, up to 1 dm long and 1 to 2 mm broad; they are often rather conspicuously septate for about the upper third of their length. The rootstock is brown in color, and it is covered with scales which may be as much as 1 cm. long.

In some respects the above specimens resemble *J. Fauriensis* Buch. var. *kamtchatcensis* Buch. from Kamtchatka. However, none of the few available specimens of *J. Fauriensis* examined have had an inflorescence with only two florets, and most inflorescences of this species have more than 10 florets. The two-flowered inflorescence of the St. Lawrence specimens seems to be typical of all specimens. The leaves of *J. Fauriensis* are normally septate for most of their length, while those of the St. Lawrence specimens are septate for only about one third of their length.

SPECIMENS EXAMINED: *Young 701*, Boxer Bay.

59. **Luzula arcuata** (Wahlenb.) Sw.

Common on most well-drained alpine and backshore areas. The specimens from St. Lawrence show a great deal of variation. A number of specimens can only arbitrarily be separated from *L. confusa*, while there are some which approach *L. Wahlenbergii* in the structure of their inflorescence. The great amount of variation in specimens of *L. arcuata* and a degree of intermediacy between *L. confusa* and *L. Wahlenbergii* raises the question as to whether *L. arcuata* may have originated by means of introgression between these two species. A situation of this type apparently occurs in the extremely complex *L. multiflora* group (Hultén, 1962). It is interesting to note that while *L. confusa* has a complete circumpolar range, both *L. arcuata* and *L. Wahlenbergii* have gaps in their ranges. *Luzula arcuata* apparently is found only where *L. confusa* and *L. Wahlenbergii* occur together. A possible exception is the Aleutian Islands. *Luzula beringensis* Tolm. and *L. unalaschcensis* (Buch.) Satake also appear to belong to the same complex (Tolmatchev, 1963), and some questionable specimens from St. Lawrence Island could, with some justification, be identified as one or the other of these species. However, it seems that a conservative treatment of this group is justified until the relationships within the entire complex can be worked out in more detail.

SPECIMENS EXAMINED: (1) More or less typical *L. arcuata: Young 127*, Tapphook; *195*, Savoonga; *283x*, *295*, Northeast Cape. (2) Approaching *L. confusa*, with

flowers tightly aggregated, pedicels rather thick: *Young 30,* Tapphook; *373,* Kialegak. (3) Approaching *L. Wahlenbergii,* with flowers in small clusters on long capillary pedicels, but with several flowers together and with narrow, involute leaves: *Young 187,* Kookooligit Mountains. Hultén (1943) also reports several collections of *L. arcuata* from St. Lawrence. Range: difficult to ascertain because of taxonomic confusion, but apparently specimens which can be referred to *L. arcuata sensu lato* are found from Spitzbergen across arctic Siberia to the Bering Sea region and south in the mountains of western North America. Northern limit: not clear, but probably zone 3.

60. **Luzula Wahlenbergii** Rupr.

Fairly common on better drained tundra and backshore areas. See *L. arcuata.*

SPECIMENS EXAMINED: *Young 62,* Tapphook; *304,* Northeast Cape; *473,* Siknik; *601,* Boxer Bay; *769, 1307,* Gambell. Range: essentially circumpolar, but rare in Greenland. Arctic. Northern limit: closely follows the northern boundary of zone 3.

61. **Luzula tundricola** Gorod.

Common on backshores and dry alpine slopes. *Luzula tundricola* was, until recently, considered to be a variety of *L. arctica,* from which it differs in a number of minor characters. The more obvious differences are that *L. tundricola* has more numerous flower heads, shorter culms, and broader leaves than *L. arctica.* Although these differences are relatively minor, they are consistent in our area. There is no doubt that two distinct taxa are involved, although there is some question in my mind as to whether the distinction should be made at the species level. *Luzula arctica sensu lato* is rather rare on St. Lawrence, and earlier reports of this species undoubtedly are referable to *L. tundricola.*

SPECIMENS EXAMINED: *Young 4,* Gambell; *103, 121, 122,* Tapphook; 283, Northeast Cape; 383, Kialegak; *640, 1336,* Boxer Bay. Range: broadly amphi-Beringean, extending from Yamal Peninsula to western Mackenzie District. Northern limit: zone 2.

62. **Luzula arctica** Blytt [*Luzula nivalis* (Laest.) Beurl.]

Rare on St. Lawrence; two stations were found in alpine areas. See *L. tundricola.*

SPECIMENS EXAMINED: *Young 788,* Gambell; *1404,* near Powooiluk. Range: circumpolar, arctic, reaching south of the high arctic only in mountainous regions. Northern limit: found throughout zone 1.

63. **Luzula confusa** Lindeb.

Common on most tundra and backshore areas. In most specimens, the spikes are closely aggregated, forming a single head (var. *eradiata* Hult.). Occasional specimens with less congested inflorescences are found, and these may approach *L. arcuata.* See *L. arcuata.*

SPECIMENS EXAMINED: *Young 106,* Tapphook; *408,* Kialegak; 533, *540,* Siknik; *780, 785, 1306,* Gambell. Several other reports. Range: circumpolar, arctic, with a few stations in alpine areas. Northern limit: found throughout zone 1.

64. **Luzula multiflora** (Retz.) Lej.

Two small stations were found in mesic tundra on the south side of the island. The specimens are low-grown and delicate, with single flower heads. They belong to the arctic montane race, which Hultén (1968a) calls var. *frigida.*

SPECIMENS EXAMINED: *Young 583,* Gaedtuk; *1330,* Boxer Bay. Also reportedly collected by Chamisso (Hultén, 1943). Range: circumpolar, low arctic and temperate regions. Northern limit: northern zone 4, reaching zone 3 in Greenland and probably in arctic Siberia.

LILIACEAE

65. **Veratrum album** L.

A single plant was found growing in mesic tundra along the upper reaches of the Koozaata River. The specimen has a narrow, spike-like inflorescence and long, narrow petals and sepals. The leaves are narrow, acute, and glabrous on both sides; it therefore belongs to ssp. *oxysepalum,* which is sometimes treated as a distinct species.

SPECIMEN EXAMINED: *Young 1345,* Nuna. No previous reports. Range: a Eurasian

species, barely reaching westernmost Alaska. Northern limit: not clear, but apparently reaches zone 3 along the arctic coast of Siberia.

66. **Lloydia serotina** (L.) Rchb.

Common to abundant in snow patch situations, grassy alpine areas, and mesic tundra. Also found on hummocks of wet tundra.

SPECIMENS EXAMINED: *Young 11*, Tapphook; *211*, Savoonga; *290*, Northeast Cape; *365*, Kialegak; *704*, Boxer Bay. Several other reports. Range: alpine areas of Europe, Asia, and western North America, also arctic Siberia and Alaska. Northern limit: zone 2.

SALICACEAE

The genus *Salix* is a notoriously difficult group, particularly in boreal and arctic regions of western North America and Eastern Siberia. On St. Lawrence Island it is not as difficult as on the Alaskan mainland, since many of the critical shrubby species such as *S. glauca* are not represented in the St. Lawrence flora. The treatment of the *Salix* species in this paper follows that of Raup (1959). This is a more conservative treatment than that of Hultén (1943, 1968a), and it seems more appropriate in such critical groups as the *S. arctica* and the *S. ovalifolia* complexes. I also follow Raup (*loc. cit.*) in placing anomalous specimens which may be of hybrid origin in the species to which they show the most morphological similarity, rather than trying to guess at the parentage of putative hybrids. Hultén (1943) lists a number of specimens from St. Lawrence as being of hybrid origin. I have seen few of these specimens and cannot judge where they would fall under the present treatment, so have not listed them. I believe that my collections of *Salix* from the island are reasonably complete and show most of the variation present but several natives have told me of areas on the interior south side where shrubs grow to a height of several feet. These shrubs might be *Salix pulchra*, but it is also possible that some of the taller shrub willows such as *S. glauca* or *S. alaxensis* will be found on the island.

67. **Salix reticulata** L.

Common on the lower alpine slopes, occasional on backshores and wet tundra. A very characteristic species which participates in the formation of hybrids rarely if at all on St. Lawrence.

SPECIMENS EXAMINED: *Young 13*, Tapphook; *173*, Savoonga; *419*, Kialegak; *602*, Boxer Bay. Several other reports. Range: nearly circumpolar, but absent in Greenland. The most widely distributed of the polar willows. Northern limit: northern zone 3, reaches lower edge of zone 2 along the coast of Siberia.

68. **Salix polaris** Wahlenb.

Common in most alpine areas. Material from the Beringean region is commonly placed under ssp. *pseudopolaris*, which is sometimes treated as a separate species. The St. Lawrence Island material is rather variable, and some of it is probably of hybrid origin. One specimen (*Young 603*) has abnormal, apparently abortive flowers and rather unusual leaves; it is doubtless a hybrid.

SPECIMENS EXAMINED: *Young 17*, Tapphook; *201x*, Savoonga; *590*, *603*, Boxer Bay; *786*, Gambell; *1444*, Ataakas Camp. *Geist*, 1933, Poovookpuk. Also reported by Kjellman (1882). Range: Arctic Eurasia and Alaska to the western Canadian arctic. Northern limit: zone 1.

69. **Salix phelbophylla** Anderss.

Common to abundant on most alpine areas. A characteristic species, easily identified by the persistent skeletonized remains of old leaves. The species is seldom involved in hybrids, but see *S. rotundifolia*.

SPECIMENS EXAMINED: *Young 105*, Tapphook; *270*, Fossil River; *284*, Northeast Cape; *375*, Kialegak; *764*, Gambell; *1409*, *1410*, near Powooiluk. The last is an unusually robust specimen with large leaves which may be a hybrid. *Geist*, 1933, Boxer Bay, Poovookpuk, Kangee, "western half." Several other reports. Range: amphi-Beringean, mainly confined to Alaska, Yukon, and eastern Siberia. Northern limit: reaches Wrangel Island and Point Barrow, in zone 2.
(*Salix rotundifolia* Trautv.)

Supposedly collected by Chamisso and Eschscholtz (Hultén, 1943). This species is closely related to S. *phlebophylla,* and intermediates between the two are common (Raup 1959). Two specimens from the Kookooligit Mountains (*Young 201; Geist,* 1933, Atuk Mountain) have the small, round leaves characteristic of S. *rotundifolia* and lack the persistant skeletonized leaves of S. *phlebophylla.* However, the ovaries are pubescent, as in S. *phlebophylla,* and it seems best to consider the above specimens as being somewhat atypical members of that species. The presence of S. *rotundifolia* on St. Lawrence is not supported by any modern specimens therefore, and the species is accordingly excluded from the island's flora.

70. **Salix arctica** Pall.

Common on alpine slopes and hummocks of wet tundra. The S. *arctica* complex is the most puzzling group of polar willows. In the vicinity of the Bering Sea, the S. *arctica* complex is divided into three taxa which are treated as subspecies: ssp. *arctica,* ssp. *crassijulis,* and ssp. *torulosa.* Although the differences between typical specimens of each of these subspecies are often striking, it is mainly the result of differences in the size and shape of leaves and catkins, and in the growth habit of the plants. When one searches for more qualitative morphological characters with which to differentiate the subspecies, one finds that a sizable array of specimens will include those that bridge any proposed lines between subspecies. Many specimens from the lowlands of St. Lawrence have the robust growth habit and orbicular leaves typical of ssp. *crassijulis,* but this form grades clinally into the more dwarfed alpine form which is usually treated as ssp. *arctica.* Some specimens in the lower alpine areas have the narrow, oblanceolate leaves which Hultén (1968a) considers to be typical of ssp. *torulosa.* There are also a number of specimens with abortive, hermaphroditic flowers which appear to resemble S. *arctica sensu lato* most closely but which are probably of hybrid origin. As less than half of the S. *arctica* specimens from St. Lawrence which I have seen can be placed easily in any one subspecies, I have made no attempt to give the subspecies of the specimens in following list.

SPECIMENS EXAMINED: *Young 15,* Tapphook; *172,* Savoonga; *461,* Kialegak; *509,* Siknik; 558, Gaedtuk; *606, 648, 682,* Boxer Bay; *768, 782,* Gambell; *Mason,* July 10, 1931, Aivichtook Lagoon. *Geist,* 1931, Savoonga; 1933, Poovookpuk, Camp "C." Several other reports. Range: nearly circumpolar, somewhat fragmented in the Atlantic regions; arctic. Northern limit: found in most zone 1 areas.

71. **Salix fuscescens** Anderss. (*S. arbutifolia* Pall.)

Common on hummocks of wet tundra. This species is easily identified because of the presence of a few gland-tipped teeth at the base of the leaf. Occasional specimens lack these teeth and may be confused with S. *ovalifolia,* which is normally a littoral species with flagelliform branches and the under surfaces of the leaves pubescent, in contrast to the leaves of S. *fuscencens,* which are glabrous on both surfaces. The leaves of dried specimens of S. *fuscescens* are usually dark brown in color.

SPECIMENS EXAMINED: *Young 306,* Northeast Cape; *547, 1382,* Gaedtuk; *659, 666,* Boxer Bay. Several other reports. Range: broadly amphi-Beringean, with isolated stations in the Hudson Bay region (Hultén 1968a). Northern limit: not clear. Reaches Point Barrow, a zone 2 area.

72. **Salix ovalifolia** Trautv.

Common on backshores and barrier beaches where it forms dense mats several feet in diameter. The S. *ovalifolia* group forms a highly variable and difficult complex which is mainly confined to coastal areas of the Beringean region. Hultén (1943) proposes a division of the complex into five species, S. *ovalifolia,* S. *flagellaris* Hult., S. *stolonifera* Cov., S. *glacialis* Anderss., and S. *arctolitoralis* Hult. All except S. *stolonifera* were thought to occur in the Beringean region. Raup (1959) in general concurs with Hultén's (*loc. cit.*) analysis. In a more recent treatment, Hultén (1968a) divides the Beringean material into two species, S. *ovalifolia* and S. *cyclophylla* Rydb. The first species is mainly confined to the northern Beringean region, the second to the more southern area. Specimens with pubescent ovaries are considered to be hybrids between S. *ovalifolia* and S. *arctica;* in earlier treatments these were considered under S. *glacialis.* Saint Lawrence Island lies in the middle of the zone of contact

between Hultén's (1968a) *S. ovalifolia* and *S. cyclophylla*. Saint Lawrence specimens of this complex are exceedingly variable, and if one had access to a limited number of specimens and had no field experience in the area, one would be tempted to treat the material as several distinct species.

There can be found dozens of individuals of the *S. ovalifolia* group on almost any sizable beach on St. Lawrence. Close examination reveals that each clump differs from its neighbors in terms of ovary size, number of flowers and size of catkin, pigmentation of the inflorescence and twigs, and size and shape of leaves. There seems to be no noticeable pattern to this variation, and I have found no significant correlations of characters. Therefore, I must conclude that only a single taxon is involved. Tolmatchev (1966b) reaches the same conclusion with respect to eastern Siberian members of the *S. ovalifolia* complex.

SPECIMENS EXAMINED: *Young 22, 24, 141,* Tapphook; *155, 167,* Savoonga; *418,* Kialegak; *530, 534,* Siknik. *Mason 6101,* Aivichtook Lagoon. *Geist,* 1933, Savoonga. Several other reports. Range: difficult to determine because of taxonomic confusion. The *S. ovalifolia* complex, including *S. ovalifolia, S. cyclophylla,* and *S. stolonifera sensu* Hultén (1968a) is found along the entire coast of Alaska and along the coast of easternmost Siberia. Northern limit: reaches the vicinity of Point Barrow, a zone 2 area.

(*Salix glacialis* Anderss.)

Considered as a hybrid between *S. ovalifolia* and *S. arctica.* I have examined one specimen (*Young 155,* Savoonga) which might be this hybrid.

73. **Salix Chamissonis** Anderss.

This species is characteristic because its leaves have serrated margins. However, of the two specimens from St. Lawrence which I have seen, one appears to be typical *S. Chamissonis,* a tundra species similar in habit to *S. arctica,* while the other was collected in a riparian gravel situation in company with *S. pulchra,* and it is similar in habit to that species. It is possible that the latter specimen may represent a hybrid between *S. Chamissonis* and *S. pulchra.*

SPECIMENS EXAMINED: *Young 94,* Kookooliktook River; *362,* Kialegak. Several other reports. Range: amphi-Beringean, generally confined to mountainous areas. Northern limit: reaches Wrangel Island, a zone 2 area.

74. **Salix pulchra** Cham.

Common to abundant on wet tundra and alpine areas where there is sufficient moisture. Also found in riparian gravel where it may reach a height of nearly two feet.

SPECIMENS EXAMINED: *Young 23, 56, 86, 87,* Tapphook and Kookooliktook River; *154,* Savoonga; *279,* Northeast Cape; *508,* Siknik. *Geist,* 1933, "western half," Camp "C." Several other reports. Range: arctic Siberia and northwestern North America. Northern limit: zone 2.

BETULACEAE

75. **Betula nana** L.

Rare on St. Lawrence, although abundant on the Alaskan mainland, where it forms an important constituent of the vegetation of shrubby tundra. No two authors agree on the taxonomy of this complex group; I follow Hultén (1968a) in considering all specimens from coastal regions of arctic Alaska as ssp. *exilis.*

SPECIMENS EXAMINED: *Young 309,* Northeast Cape; *380,* Kialegak; *548,* Gaedtuk. Also reportedly collected by Coville and Kearney (Hultén 1944). Range: *Betula nana sensu lato:* circumpolar, arctic-alpine. Northern limit: closely follows the northern edge of zone 3.

POLYGONACEAE

76. **Koenigia islandica** L.

Locally common in ephemeral pools, puddles and wet spots, particularly in waterfowl nesting areas and near old village sites. Appears to be somewhat nitrophilous.

SPECIMENS EXAMINED: *Young 237,* Savoonga; *673,* Boxer Bay; *1475,* Kookoolik. Several other reports. Range: circumpolar, arctic-alpine. Appears to be somewhat

fragmented and probably fluctuates somewhat in the course of time, since the plant is an annual. Northern limit: zone 3, occasionally reaching zone 2.

77. **Rumex graminifolius** Lamb.

Found at a single station on a moist alpine slope at low elevation.

SPECIMENS EXAMINED: *Young* 79, Tapphook. No previous reports. Range: arctic and alpine regions of Eurasia and western Alaska; apparently rare throughout its range. Reported from northeast Greenland by Böcher *et al.*, 1957. Northern limit: not clear, but reaches Wrangel Island, a zone 2 area.

78. **Rumex acetosa** L.

A few specimens were collected on the banks of the upper reaches of the Koozaata River. The specimens appear to be the typical artic-montane form which Hultén (1968a) treats as ssp. *alpestris*, and which corresponds to the forms treated as ssp. *lapponicus* and ssp. *pseudoxyria* by Tolmatchev (1966b).

SPECIMENS EXAMINED: *Young 1349*, Nuna. Also reportedly collected by Geist (Hultén 1944). Range: the nominate subspecies is widely distributed throughout the world, often occurring as an introduced weed. Subspecies *alpestris* ranges across Eurasia in arctic and alpine regions, reaching Alaska and the northern Rocky Mountains. Northern limit: closely follows the northern edge of zone 3 in Siberia; reaches Wrangel Island, a zone 2 area.

79. **Rumex arcticus** Trautv.

Common or abundant on backshores and at the edges of small ponds and puddles on wet tundra. Common on moist alpine slopes.

SPECIMENS EXAMINED: *Young 16*, Tapphook; *166*, Savoonga; 323, Northeast Cape; *434*, Kialegak; *624*, Boxer Bay; *771*, Gambell. Several other reports. Range: arctic Siberia and northwestern North America. Northern limit: reaches at least to southern zone 2.

80. **Oxyria digyna** (L.) Hill

Common to abundant on rocky streambanks, alpine areas, and hummocks on wet tundra. The raw foliage is edible; it has a pleasant, sour flavor and makes a good thirst quencher. It is particularly useful on St. Lawrence Island, since most water sources on the island are infested with *Echinococcus multilocularis*, and the water is unsafe to drink without boiling.

SPECIMENS EXAMINED: *Young 12*, Tapphook; *185*, Savoonga; *291*, Northeast Cape; 379, Kialegak; *607*, Boxer Bay; *777*, Gambell. Many other reports. Range: circumpolar, arctic-alpine. One of the most ubiquitous arctic plants. Northern limit: found throughout zone 1.

81. **Polygonum viviparum** L.

Common where there is adequate moisture. The material from St. Lawrence is extremely variable in terms of growth habit, leaf shape and thickness, flower color, and length of time during which the bulblets are retained on the parent plant. This species normally reproduces apomictically, which could account for the variation. Some specimens have some of the characters of *P. bistorta*, but since sexually reproducing populations of *P. vivipara* are not known, it seems unlikely that the species is involved in any hybrids.

SPECIMENS EXAMINED: *Young* 355, Northeast Cape; *339*, *445*, Kialegak; *502*, Siknik; *578*, *599*, Boxer Bay; *734*, Gambell. *Anderson 5153b*, Savoonga. Also reported by Kjellman (1882). Range: circumpolar, arctic-alpine. Northern limit: reaches the northern edge of zone 2.

82. **Polygonum bistorta** L.

Rare on St. Lawrence; a few stunted specimens were collected in alpine seepage areas, often at rather high elevation.

SPECIMENS EXAMINED: *Young* 39, Tapphook; 389, Kialegak; *693*, Boxer Bay. No other reports. Range: widely distributed in arctic and alpine regions of Eurasia; reaches Alaska and extreme northeastern Canada. Northern limit: barely reaches zone 2.

PORTULACACEAE

83. **Claytonia acutifolia** Pall.

Uncommon in snow patches and alpine seepage areas. The St. Lawrence Island material is variable. The majority of specimens belong to the form treated as ssp. *graminifolia* by Hultén (1968b), but some specimens more nearly approach ssp. *acutifolia*. Since the variation between these two forms appears to be continuous, I concur with Hultén (1968b) that they should be considered under the same species. However, Davis (1966) and Tolmatchev (1966b) treat the two forms as distinct species.

SPECIMENS EXAMINED: *Young 619*, Boxer Bay; *773*, Gambell. *Mason 6104*, Aivichtook Lagoon. Range: arctic and alpine regions of eastern Siberia and Alaska. Northern limit: reaches zone 2 at Wrangel Island.

(*Claytonia tuberosa* Pall.)

This species has been reported twice from St. Lawrence. Hultén (1944) mentions a specimen supposedly collected by Haley in 1926. As mentioned, there is some question as to the reliability of the collection location of Haley's labels. Davis (1966) identified a specimen of Anderson's (*3669b*, ISU) as *C. tuberosa*. As Hultén (1944) lists this same specimen under *C. sarmentosa*, it seems safe to assume that the specimen referred to by Davis is mixed with *C. sarmentosa*, and there is some doubt as to whether the identification is correct. During two summers of field work on St. Lawrence, I was never able to find any plant which could possibly be mistaken for *C. tuberosa*. Therefore, I conclude that the species does not occur on the island or is extremely rare. It is excluded from the flora until its occurrence on the island can be substantiated.

84. **Claytonia arctica** Adams

Collected once, high on a barren cinder cone at the edge of the Kookooligit Range.

SPECIMENS EXAMINED: *Young 1430*, Ataakas Camp. No previous reports. Range: arctic eastern Siberia and the islands of the Bering Sea. Not yet known to occur on the mainland of Alaska (Davis 1966). Northern limit: reaches Wrangel Island, in zone 2.

85. **Claytonia sarmentosa** C. A. Mey.

Common to abundant on old village sites, bird cliffs. Less common on hummocks of wet tundra and snow beds on alpine slopes.

SPECIMENS EXAMINED: *Young 64, 128*, Tapphook; *159*, Savoonga; *293, 336*, Northeast Cape; *439*, Kialegak; *494*, Siknik; *634*, Boxer Bay. Several other reports. Range: Alaska, Yukon, and a few stations in eastern Siberia. Northern limit: not clear, probably zone 3.

86. **Montia fontana** L.

Occasional on bare soil on wet areas, particularly in old village sites and areas where waterfowl congregate. Often associated with *Koenigia islandica*, the only other annual native to St. Lawrence.

SPECIMENS EXAMINED: *Young 138*, Tapphook; *169x*, Savoonga; *736x*, Gambell. Also reportedly collected by Anderson (Hultén 1944). Range: circumpolar, but rather fragmented; arctic and temperate regions, including stations in the southern hemisphere. Northern limit: reaches zone 3 in some areas.

CARYOPHYLLACEAE

87. **Stellaria humifusa** Rottb.

Common on backshores and near lagoons. Occasionally found on foreshores.

SPECIMENS EXAMINED: *Young 169*, Tapphoook; *341, 353*, Northeast Cape; *736, 737*, Gambell. Several other reports. Range: circumpolar, mostly in arctic, but south along the coast to some temperate regions. Northern limit: zone 2, reaching zone 1 in a couple of stations.

88. **Stellaria crassifolia** Ehrh.

Occasional in ephemeral pools and puddles, bare soil areas, sandy shores of small lakes, and particularly on river bars subject to occasional flooding. Specimens with

mature capsules were not collected. One or two of the specimens listed under S. *humifusa* may belong to S. *crassifolia*.

SPECIMENS EXAMINED: *Young 754*, Gambell; *1384*, Gaedtuk. Also reportedly collected by Anderson (Hultén 1944). Range: circumpolar, somewhat fragmented, arctic-alpine. Northern limit: zone 3, reaching zone 2 at Point Barrow.

89. **Stellaria Edwardsii** R. Br. (*S. ciliatosepala* Trautv.)

Rather rare on backshores, rocky stream banks, and ravines in raised beaches. All St. Lawrence specimens of the difficult *S. longipes* complex are best identified as *S. Edwardsii*, although the ciliated margins of the sepals are not always particularly evident.

SPECIMENS EXAMINED: *Young 227*, Savoonga; *432*, Kialegak; *541*, Siknik; *1319*, Boxer Bay; *789x*, *1304*, Gambell. No previous reports. Range: circumpolar, arctic. Northern limit: zone 1.

90. **Cerastium Beeringianum** Cham. and Schlecht.

Common on backshores, along stream banks and other sandy areas. Occasional on drier alpine slopes. The material from St. Lawrence is extremely variable in terms of growth habit and flower size, but most specimens have the retrorse, stiff hairs on the lower internodes which Hultén (1956) maintains is characteristic of *C. Beeringianum*. Hultén (*loc. cit.*) considers Alaskan material of this species as belonging to ssp. *Beeringianum*, but he distinguishes two varieties, var. *grandiflorum* and the nominate variety, on the basis of comparative length of the petals. The two varieties are listed separately below, but the distinction is not always clear. Variety *grandiflorum* is most commonly found on shore areas, while var. *Beeringianum* is more common in stream beds and alpine areas. The distinction between *C. Beeringianum* var. *grandiflorum* and *C. jenisejense* Hult. is not very clear, and some specimens listed below might be treated under the latter species. A single specimen (*Young 1438*) from an alpine lava field differs from all others in its densely cespitose growth habit. In some respects this specimen approaches the published descriptions of *C. aleuticum*, but it also has many of the characters of *C. Beeringianum*, and it is probably best identified as that species.

SPECIMENS EXAMINED: var. *Beeringianum: Young 235*, *1447*, Savoonga; *431*, Kialegak; *491*, Siknik; *1438*, Ataakas Camp. Variety *grandiflorum: Young* 289, Northeast Cape; *394*, Kialegak; *487*, Siknik; *567*, Gaedtuk; *633*, *639*, Boxer Bay. Several other reports. Range: arctic Siberia, Alaska, and Canada, south in mountainous areas. Apparently intergrades with other members of the *C. alpinum* complex in areas of contact, and the exact range is difficult to delineate. Northern limit: members of the *C. alpinum* complex reach the northern limit of land in all parts of the arctic. Since there are no zone 1 areas within the main part of the range of *C. Beeringianum*, the potential northern limit of that species is not certain. It definitely reaches into zone 2.

91. **Sagina intermedia** Fenzl.

Common on backshores, at the edges of lagoons, and on old house and village sites. Apparently somewhat nitrophilous.

SPECIMENS EXAMINED: *Young 139*, Tapphook; *236*, Savoonga; *352*, Northeast Cape; *452*, Kialegak; *544*, Siknik; *668*, Boxer Bay. Other reports. Range: circumpolar, arctic. Northern limit: reaches zone 1 on Franz Josef Land and New Siberian Island.

92. **Minuartia macrocarpa** (Pursh) Ostenf.

Occasional on most of the drier areas of the island. The specimens treated here as *M. macrocarpa* all have rather broad leaves with three or more nerves, and usually with well-developed marginal cilia. Undamaged capsules are usually more than 10 mm long, but the old capsules are fragile and often broken up, so that the large ones are sometimes of no use in identifying this species. Plants are usually loosely cespitose or trailing. A thin, semi-woody taproot may or may not be present.

SPECIMENS EXAMINED: *Young 31*, Tapphook; *267*, Fossil River; *511*, Siknik; *648*, Boxer Bay. Several other reports. Range: arctic and alpine regions of Siberia and Alaska. Northern limit: occurs in some zone 2 areas.

93. **Minuartia arctica** (Stev.) Aschers. and Graebn.

Occasional, sometimes common on backshores, fell-fields, rocky alpine areas, and other well-drained habitats. This is a variable and difficult species which grades toward *M. macrocarpa* on one hand and *M. obtusiloba* on the other. I have placed all specimens with involute, single-nerved or nerveless leaves in *M. arctica,* with the exception of a single specimen treated under *M. obtusiloba.* Most specimens considered under *M. arctica* are loosely cespitose and are herbaceous, although some individuals may have a woody taproot. In most specimens the capsule is 5–8 mm long, but a few individuals which appear to be intermediates between *M. arctica* and *M. macrocarpa* may have capsules up to 10 mm long.

SPECIMENS EXAMINED: *Young 192,* Savoonga; *288,* Northeast Cape; *572, 1368,* Gaedtuk; *702, 720,* Boxer Bay. *Geist,* 1933, Boxer Bay. Range: arctic and alpine areas in Siberia and Alaska. Northern limit: not clear; reaches at least to northern zone 3.

94. **Minuartia obtusiloba** (Rydb.) House

Found once on a dry sea cliff near Boxer Bay. This species is similar to *M. arctica,* but it has a densely cespitose habit, a thick, woody taproot, somewhat woody branches, and short, imbricated leaves which are sometimes ciliated nearly to the apex. Some of the specimens treated under *M. arctica* approach *M. obtusiloba* in terms of growth habit.

SPECIMENS EXAMINED: *Young 647,* Boxer Bay. No previous reports. Range: the Beringean regions and the mountains of western North America. A closely related or identical species occurs in the Gulf of St. Lawrence region in eastern Canada [*M. marcescens* (Fern.) House].

95. **Honckenya peploides** (L.) Ehrh.

Common on foreshores. Usually associated with *Mertensia maritima,* both species being found to the seaward of the *Elymus* zone. All St. Lawrence specimens are of prostrate growth habit.

SPECIMENS EXAMINED: *Young 129,* Tapphook; *344,* Northeast Cape; *462,* Kialegak; *495,* Siknik; *653,* Boxer Bay. Several other reports. Range: circumpolar, but in common with most strand species rare along the arctic coast of Siberia. Northern limit: zone 3.

96. **Wilhelmsia physodes** (Fisch.) McNeill

Occasional in sandy stream beds, on solifluction lobes, and on raised beaches.

SPECIMENS EXAMINED: *Young 584,* Gaedtuk; *726, 743,* Gambell. Several other reports. Range: easternmost Siberia and northwestern North America. Northern limit: zone 3.

97. **Silene acaulis** L.

Occasional on rocky areas, particularly small alpine stream beds.

SPECIMENS EXAMINED: *Young 176,* Savoonga; *442,* Kialegak; *532x,* Siknik. Several other reports. Range: arctic and alpine areas of North America and Europe. Hardly known from Siberia. Northern limit: reaches zone 1 in Franz Josef Land.

98. **Melandrium apetalum** (L.) Fenzl

Fairly common on moist tundra, snow patches, and lower alpine slopes. The taxonomy of the arctic members of the genus *Melandrium* is still not clearly understood, and most of the published keys to the genus are confusing. The often used characters of seed size and wing shape on the seed are useful, but may be confusing. The seeds apparently turn brown before they have reached their mature size and configuration, so that it is not always possible to tell whether a specimen has mature seeds or not. On St. Lawrence, there are two distinct forms within the genus *Melandrium.* The form treated here as *M. apetalum* is usually confined to moist tundra and is not found on backshores or other dry areas. The flowers are usually borne singly on stems up to 2 dm tall. Flowers are most frequently nodding at anthesis, but they soon afterwards become erect, and this character seems to be of little taxonomic value. The capsule opens with five teeth, but each tooth has a suture down the center which may occasionally break open and cause the apex of

the capsule to appear ten-toothed. The mature seeds are about 2 mm in diameter, with a broad wing. Some of the specimens treated here as *M. apetalum* could, with some justification, be identified as *M. macrospermum*, a rare and somewhat indistinct species found only in extreme northwestern North America.

SPECIMENS EXAMINED: *Young 104*, Tapphook; *251*, Savoonga; *562*, Gaedtuk; *1317*, Boxer Bay. Several other reports. Range: circumpolar, arctic-alpine. Northern limit: closely follows the northern edge of zone 2. Reaches zone 1 in Severnaya Zemlya according to Hultén (1968a).

99. **Melandrium affine** J. Vahl

Common, sometimes abundant on pebble beaches, backshores; occasional on dry slopes. The St. Lawrence specimens vary widely in the color of the corolla, which may range from white to deep violet. Hultén (1944) treats the specimens with violet petals as a separate species, *M. Soczavaenum* Schischk. Since the total range of variation between the two colors can sometimes be found on a few square feet of backshore, it seems unlikely that the difference in color is of much taxonomic significance. The purple form generally predominates on St. Lawrence, and its description as a variety of *M. affine* might be warranted.

SPECIMENS EXAMINED: *Young 410, 421*, Kialegak; *507*, Siknik; *698*, Boxer Bay. Range: circumpolar, arctic-alpine. Northern limit: closely follows the northern edge of zone 2.

RANUNCULACEAE

100. **Caltha palustris** L.

Common in shallow pools on backshores and raised beaches, occasional on wet tundra. Saint Lawrence specimens belong to var. *arctica*.

SPECIMENS EXAMINED: *Young 58, 108*, Tapphook; *149*, Savoonga; *289*, Northeast Cape; *417*, Kialegak; *516*, Siknik; *697*, Boxer Bay. Several other reports. Range: nearly circumpolar, absent in Greenland. Arctic and cool temperate regions. Northern limit: var. *arctica* reaches northern zone 2.

101. **Delphinium brachycentrum** Ledeb.

Found on the sides of several steep-sided valleys near Southwest Cape. Usually grows on scree slopes or on rock outcrops.

SPECIMENS EXAMINED: *Young 594*, Kangee. *Geist*, 1933, Poovookpuk. Range: mountainous areas in northwestern North America and northeastern Siberia. Northern limit: not clear, but probably zone 3.

102. **Aconitum delphinifolium** DC.

Abundant on mesic tundra and backshores in the vicinity of ancient or modern human habitations; rare in alpine snow flushes. Hultén (1968a) indicates that both ssp. *paradoxicum* and ssp. *delphinifolium* occur on St. Lawrence. All specimens which I have seen have the low growth and single flower typical of ssp. *paradoxicum*.

SPECIMENS EXAMINED: *Young 216*, Savoonga; *632*, Boxer Bay; *730*, Gambell. Several other reports. Range: northeastern Siberia and northwestern North America. Northern limit: reaches Wrangel Island, in zone 2.

103. **Anemone narcissiflora** L.

Common on backshores and moist tundra, occasional in lower alpine areas. All St. Lawrence Island specimens belong to ssp. *sibirica*.

SPECIMENS EXAMINED: *Young 10*, Gambell; *33*, Tapphook; *212*, Savoonga; *370*, Kialegak; *617*, Boxer Bay; *1364*, Gaedtuk. Several other reports. Range: many disjunct areas in mountainous parts of Europe and Asia, some stations in western North America south of Alaska. Hardly reaches the arctic outside our area. Northern limit: reaches Wrangel Island, zone 2.

104. **Anemone Richardsonii** Hook.

Common along stream banks, on solifluction lobes, and in other mesic tundra situations.

SPECIMENS EXAMINED: *Young 84*, Tapphook; *243*, Savoonga; *367*, Kialegak; *705*, Boxer Bay. Other reports. Range: essentially an expanded amphi-Beringean distribu-

tion, with a few stations as far east as eastern Canada and Greenland. Northern limit: zone 3.

105. **Ranunculus aquatilis** L.

Found in small streamside pools near Gaedtuk. I am unable to equate the St. Lawrence specimens with any of the North American varieties of *R. aquatilis* discussed by Benson (1948). The most striking character of the St. Lawrence specimens is the large fruiting head, each containing 30 to 50 achenes which are approximately 2 mm long in the mature condition, and hispidulous along the suture. These characters should exclude the specimens from var. *eradicatus* [*R. confervoides* (E. Fries) E. Fries], the member of the *R. aquatilis* complex which is most commonly found in arctic regions. In some respects the St. Lawrence specimens approach var. *capillaceus* (*R. trichophyllus* Chaix.) but the achenes are both larger and more numerous than is usual in this form. I am inclined to consider the St. Lawrence material as being a somewhat aberrant form of var. *capillaceus*, but if more material were available it is quite possible that the creation of a new variety would be justified.

SPECIMENS EXAMINED: *Young 1341*, Gaedtuk. No previous reports. Range: (*R. aquatilis sensu lato*): circumpolar, widely distributed in both temperate and arctic regions, and reaching the southern hemisphere. Northern limit: appears to follow fairly closely along the northern boundary of zone 3, with some stations in zone 2.

106. **Ranunculus Gmelini** DC.

Found in a few shallow puddles near Gaedtuk. The St. Lawrence specimens appear to be intermediate between ssp. *Gmelini* and ssp. *Purshii* (Richards.) Hult.

SPECIMENS EXAMINED: *Young 1355*, Gaedtuk. No previous reports. Range: nearly circumpolar, but not known in the arctic regions bordering the Atlantic Ocean; arctic, alpine, and cool temperate regions. Northern limit: not clear; some stations as far north as zone 2.

107. **Ranunculus hyperboreus** Rottb.

Common in shallow tundra pools, particularly in backshore areas where resting waterfowl increase soil fertility. Most specimens are sterile, with long, slender petioles. These specimens apparently are ssp. *hyperboreus*. A single specimen from the vicinity of Northeast Cape (*Young 354*) was collected in flower. This specimen has the tiny leaves and trailing growth habit of ssp. *Arnellii*, a high arctic form whose main range is in northern Siberia.

SPECIMENS EXAMINED: *Young 143*, Tapphook; *354*, Northeast Cape; *455*, Kialegak; *527*, Siknik. Other reports. Range: circumpolar, arctic-alpine. Northern limit: northern zone 2, a few stations in zone 1.

108. **Ranunculus Pallasii** Schlecht.

Occasional in stagnant tundra and backshore pools. Saint Lawrence specimens are of rather delicate habit, and the leaves are entire or only slightly lobed.

SPECIMENS EXAMINED: *Young 321*, Northeast Cape; *386*, Kialegak; *489*, Siknik; *601*, Boxer Bay. *Coville & Kearney 1971*, Northeast Cape. Also reported by Kjellman (1882). Range: more or less circumpolar, but in several disjunct areas. Almost entirely confined to arctic regions. Northern limit: zone 3.

109. **Ranunculus glacialis** L.

Occasional on wet tundra; of fairly regular occurrence on alpine seepage areas. Saint Lawrence specimens are usually classified as ssp. *Chamissonis*, in common with others from the Beringean region. I can see no essential difference between these specimens and those from the Atlantic range of the species, although there may be somewhat more variation in Beringean populations. Those of St. Lawrence are of comparatively robust growth habit, rather densely pubescent, and have leaves somewhat less deeply lobed than in the nominate subspecies.

SPECIMENS EXAMINED: *Young 63*, Tapphook; *615*, Boxer Bay; *804*, Gambell. *Fay & Rausch* (no date or number). Also reported by Kjellman (1882). Range: remarkably disjunct; found in the Bering Strait region, Greenland, Scandanavia, Spitzbergen, and in the mountains of central and western Europe. Northern limit: zone 3.

110. **Ranunculus reptans** L. (*R. flammula* L. var. *filiformis* (Michx.) Hook.

Found growing in shallow streamside pools near Gaedtuk; associated with *R. Gmelini*.

SPECIMENS EXAMINED: *Young 1387*, Gaedtuk. No previous reports. Range: circumpolar; arctic and cool temperate regions. Northern limit: zone 4, reaching zone 3 in a few areas.

111. **Ranunculus nivalis** L.

Common in most alpine and mesic tundra situations. *Ranunculus nivalis* is closely related to *R. sulphureus* Soland. and intermediates are not uncommon (Benson 1948, 1954). The two species are distinguished by the hairy receptable and more robust growth of *R. sulphureus*. None of the St. Lawrence specimens have well developed hairs on the receptacle, although in several cases a few hairs are definitely present. I am not wholly satisfied with my identification of these two species, and it may be that the material treated here as *R. sulphureus* is better identified as *R. nivalis*.

SPECIMENS EXAMINED: *Young* 2, Gambell; *395, 453*, Kialegak; *621*, Boxer Bay; 778, Gambell. Several other reports. Range: circumpolar, hardly occuring south of the high arctic. Northern limit: northern zone 2, reaching zone 1 in some areas.

112. **Ranunculus sulphureus** Soland.

Occasional on tundra; apparently prefers somewhat drier conditions than *R. nivalis*. See under that species.

SPECIMENS EXAMINED: *Young 20*, Tapphook; *240*, Savoonga; *280*, Northeast Cape. Also reportedly collected by Haley (Hultén, 1944). As noted, there is some doubt about the accuracy of the labeling of Haley's specimens. Range: circumpolar, mainly confined to the high arctic. Northern limit: zone 1.

113. **Ranunculus pygmaeus** Wahlenb.

Common in alpine areas and near small tundra pools. Often abundant at old village sites, near bird cliffs, and in other areas of rich, moist soils.

SPECIMENS EXAMINED: *Young 6*, Gambell; *78*, Tapphook; 233, Savoonga; *490*, Siknik; *629*, Boxer Bay. Several other reports. Range: circumpolar, arctic, with a few alpine stations in both hemispheres. Northern limit: zone 1.

114. **Ranunculus pedatifidus** J. E. Smith (*R. affinis* R. Br.)

A single specimen found on wet tundra near Tapphook appears best identified as this species. It differs from typical specimens in that the pubescence on the sepals is brownish, as in *R. sulphureus* and *R. nivalis*. The pubescence is finer and more sparse than in either of the above species and the sepals themselves are very delicate, as seems to be characteristic of *R. pedatifidus*. Vegetative characters of the above specimen fall within the range of variation of *R. pedatifidus*, an extremely variable species. The specimens mentioned above could be a hybrid between *R. pedatifidus* and *R. sulphureus* or *R. nivalis*.

SPECIMEN EXAMINED: *Young 107*, Tapphook. No previous reports. Range: circumpolar, arctic-alpine. Northern limit: lower zone 2.

(*Ranunculus repens* L.)

Benson regards *Mason 6094*, from Savoonga as a specimen of this species, which is usually an introduced weed, having originated in temperate regions. See *R. Turneri*.

115. **Ranunculus Turneri** Greene

There is considerable confusion regarding the taxon (or taxa) here considered as *R. Turneri*. The only previous report of *R. Turneri* from St. Lawrence is by Hultén (1944), who lists *Mason 6094*, Savoonga, as this species. Benson (1948) regards the same specimen as being the typical form of *R. repens*. This identification seems questionable for several reasons, the most important being that *R. repens* is generally confined to temperate regions.

My own collections contain two sets of specimens which might be regarded as *R. Turneri*, although specimens from the two collections differ considerably from each other in overall appearance. *Young 244* was collected on mesic tundra near Savoonga; it is certainly one of the most beautiful of the tundra wild flowers that occur on St. Lawrence. Individual plants are 5 cm or less tall, and each bears a single flower,

which may be nearly 3 cm in diameter. The petals are bright glossy yellow, very broad, often somewhat emarginate, and with a translucent area at the base. The nectary flaps are rudimentary and appear to be little more than thickened areas at the bases of the petals. The specimens are all too young to show achene characters clearly. The basal leaves are parted in three, with each division cleft in three to five lobes. In general appearance, the specimens mentioned above resemble the illustration of *R. Turneri* given by Hultén (1968a).

A second group of specimens (*Young 1345*) was collected on a gravel bar in a small river near Gaedtuk. These specimens are tall and robust, reaching a height of 3 to 4 dm. The flowers are somewhat smaller than those of the specimens listed above, and seldom more than 2 cm in diameter. The petals are comparatively narrow, not glossy, and have a well-developed triangular nectary flap. The achenes are about 3 mm long, with a curved, hooked beak about 1 mm long. The specimens in this collection appear to be an almost perfect match for *R. acriformis* A. Gray, a species known from the Rocky Mountains in northern United States. The hooked beak of the achene seems to be particularly characteristic of this species.

I have see only one specimen of *R. Turneri* identified by Benson (*Townsend*, 1886, Hall Island); it is quite similar to my *1345* mentioned above, although the flowers are somewhat larger. The nectary flaps in Townsend's specimen are rather large, a character which should, according to the key given by Benson (1948) exclude it from *R. Turneri.*

It appears that, in a few scattered areas of the western American arctic, populations of the *R. occidentalis* complex have persisted *in situ* during the last glacial maximum. These relict populations are rare, and they consist of relatively few individuals. During the period of time that they were isolated from the main body of the *R. occidentalis* group, they developed a considerable amount of morphological diversity. There is little chance of gene interchange between the relict populations in the far north. The name *R. Turneri,* therefore, covers a group of populations which are widely disjunct and are probably not much more closely related to each other than they are to some of the more southern populations of the *R. occidentalis* group. Apparently one or more of these populations have persisted on St. Lawrence, and specimens from my two collections, as well as the specimen of Mason belong to these populations.

The taxonomic difficulties here are obvious. One cannot clarify the taxonomy of the group with the small number of specimens available. Therefore, I consider all specimens of this group from St. Lawrence under *R. Turneri,* although it is doubtful that this is a single taxonomic entity. A good case could be made for considering *Young 1345* as *R. acriformis* and *Young 244* as either *R. Turneri* or perhaps as an undescribed species.

116. **Thalictrum alpinum L.**

Occasional in moist alpine areas and along some streambanks and solifluction lobes.

SPECIMENS EXAMINED: *Young 112,* Tapphook; *576,* Gaedtuk. Also reportedly collected by Mason (Hultén 1944). Range: essentially circumpolar, but consisting of many disjunct populations throughout arctic and alpine regions of the northern hemisphere. Northern limit: zone 3, reaching zone 2 at Wrangel Island.

PAPAVERACEAE

117. **Papaver Macounii** Greene

Occasional, most commonly found on moist alpine slopes and on solifluction lobes. The taxonomy of the arctic species of *Papaver* has been widely discussed, but no general agreement has been reached on the delineation of species and subspecific taxa within the group. On St. Lawrence there appear to be two populations of *Papaver;* they can be distinguished morphologically and usually are found on differing habitats. The group of specimens here treated as *P. Macounii* have elongated capsules with the stigmatic disk more or less conical. The leaves are grey-green, and most of the vegative parts of the plant are sparsely covered with thick, brown hairs. There is little variation within this group of specimens.

SPECIMENS EXAMINED: *Young 42,* Tapphook; *178,* Kookooligit Mountains; *800,*

Gambell; *1329*, Boxer Bay; *1438*, Ataakas Camp. Several other reports. Range: not clear, apparently confined to the Beringean region. Northern limit: not clear, but closely related species are found throughout the arctic, including all of zone 1.

118. **Papaver sp.** (aff. *Papaver radicatum* Rottb.)

Populations of *Papaver* found on drier alpine areas and sandy barrier beaches, differ considerably from the specimens enumerated under *P. Macounii*. The major difference is in the form of the capsule; the specimens listed below have a nearly spherical capsule with a broad, flat stigmatic disk, in contrast to the spindle-shaped capsule of the specimens listed under *P. Macounii*. The plants are rather densely cespitose, and usually taller and more vigorous appearing than *P. Macounii*. The leaves are olive green in color and the pubescence is usually more dense than in *P. Macounii*. It is probably an unusually small specimen of the form discussed here which Hultén (1968a) lists as *P. alaskanum* from St. Lawrence.

SPECIMENS EXAMINED: *Young 198*, Kookooligit Mountains; *545*, barrier beach 5 miles west of Siknik; *1435*, Ataakas Camp. Range: not clear. *Papaver radicatum sensu lato* is a circumpolar arctic-alpine species.

(*Papaver Walpolei* A. E. Pors.)

Hultén (1945) says that a single leaf collected at Punuk Islands by Haley probably belongs to this species. *Papaver Walpolei* is distinctive because of its white flowers, but I have never observed it growing on either the Punuk Islands or St. Lawrence. Arctic representatives of the genus *Papaver* are difficult to identify under the best of conditions, and it is pointless to include *P. Walpolei* in the St. Lawrence flora on the basis of one leaf, particularly as there is some question as to the accuracy of the labeling.

119. **Corydalis pauciflora** (Steph.) Pers.

Occasional on moist alpine slopes, solifluction lobes, etc.

SPECIMENS EXAMINED: *Young 109*, Tapphook; *238*, Savoonga; *444*, Kialegak; *587*, Boxer Bay. Several other reports. Range: alpine areas of eastern Asia and northwestern North America. Northern limit: not clear, reaches zone 3 in several places.

CRUCIFERAE

120. **Cochlearia officinalis** L.

This species is strongly nitrophilous; it is abundant and of very rank growth on bird cliffs and old village sites. It is common on backshores and barrier beaches, but almost unknown on tundra and alpine areas. Saint Lawrence specimens vary considerably in terms of growth habit, size of leaves, and shape of the silicle. Most of the variation appears to be ecologically induced, depending on the fertility of the soil. In most specimens the silicle is elliptic, but in some cases it may be globose. Hultén (1968a) believes that two subspecies can be distiguished by this character, but the distinction does not seem to be clear in the case of St. Lawrence specimens.

SPECIMENS EXAMINED: *Young 26*, Tapphook; *164*, Savoonga; *347*, Northeast Cape; *420*, Kialegak; *475*, Siknik; *667*, Boxer Bay. Many other reports. Range: circumpolar, almost entirely confined to the arctic, but also found on the Falkland Islands. Northern limit: found throughout zone 1.

121. **Eutrema Edwardsii** R. Br.

Occasional; usually found in rocky alpine areas and particularly along rocky stream banks.

SPECIMENS EXAMINED: *Young 41, 126*, Tapphook; *416*, Kialegak; *592*, Boxer Bay; *1358*, Gaedtuk. Several other reports. Range: circumpolar, mainly arctic, but also found in the mountains of central Asia. Northern limit: zone 2.

122. **Cardamine bellidifolia** L.

Common in virtually all terrestrial habitats on St. Lawrence.

SPECIMENS EXAMINED: *Young 9*, Gambell; *48*, Tapphook; *221*, Savoonga; *337*, Northeast Cape; *722*, Boxer Bay; *1370*, Gaedtuk. Many other reports. Range: circumpolar, arctic-alpine. Northern limit: found throughout zone 1.

123. **Cardamine pratensis** L.

Common on wet tundra, at the edges of pools in backshore areas and in alpine seepage areas.

SPECIMENS EXAMINED: *Young 224*, Savoonga; *404*, Kialegak; *504*, Siknik; *661*, Boxer Bay. Several other reports. Range: circumpolar, arctic, alpine, and cool temperate regions. Northern limit: zone 2.

(*Cardamine umbellata* Greene)

Reportedly collected on St. Lawrence by Haley (Hultén 1945). I have never found this rather characteristic species on the island. The possibility that Haley's labels are inaccurate has already been mentioned, and it seems doubtful that the species occurs on St. Lawrence.

124. **Cardamine microphylla** Adams

Rare; found twice on wet tundra near Savoonga.

SPECIMENS EXAMINED: *Young 184*, near Savoonga; *1443*, Kookoolik. No previous reports. Range: found in a few scattered locations in eastern Siberia and northern Alaska. Northern limit: not clear because of restricted range.

125. **Cardamine purpurea** Cham. and Schlecht.

Occasional in alpine seepage areas. All specimens have the deep purple flowers characteristic of the typical form of the species.

SPECIMENS EXAMINED: *Young 45*, Tapphook; *709*, Boxer Bay. *Mason 1931*, Aivichtook Lagoon. The type specimen was collected on St. Lawrence by Chamisso. Range: known only from central and western Alaska and western Yukon. Northern limit: not clear because of limited range.

126. **Draba nivalis** Liljebl.

A single specimen found along a dry streambank has leaves pubescent with the stellate hairs characteristic of this species. Some of the siliques have a faint pubescence, but otherwise the specimens seem to be typical *D. nivalis*.

SPECIMENS EXAMINED: *Young 1369*, Gaedtuk. No previous reports. Range: essentially circumpolar, but disrupted in Siberia; zone 2.

(*Draba pilosa* Adams ex DC.)

Hultén (1945) lists a single specimen reportedly collected from St. Lawrence (collector unspecified) that was identified by Pohle as *D. pilosa*. This species is similar to *D. lactea*, and in a group as critical as the genus *Draba* the report cannot be accepted until it is substantiated by a recent specimen.

(*Draba pseudopilosa* Pohle)

Reportedly collected by Chamisso and Eschscholtz (Hultén 1945). This species is also closely related to *D. lactea*, and the report is doubtful for the same reasons as given under *D. pilosa*.

127. **Draba lactea** Adams

Fairly common on rocky outcrops and in dry stream beds in the southwestern portion of the island. There is some variation in the material, particularly in the type and density of the pubescence of the leaves. Most specimens have both simple and stellate hairs on the leaves and would be placed in typical *D. lactea* according to most treatments. A few specimens have the stellate hairs lacking or nearly so, as is typical of *D. fladnizensis*. Abnormal specimens with a few hairs on the upper part of the scape may be responsible for the single report of *D. pseudopilosa* from St. Lawrence. There seems to be no reason to believe that more than a single population of this group exists on the island.

SPECIMENS EXAMINED: *Young 596*, Kongee; *723*, *1314*, *1334*, Boxer Bay; *1380*, Gaedtuk. Also reportedly collected by Geist at Savoonga (Hultén 1945). Range: circumpolar, arctic, zone 2, reaching zone 1 in Canada.

(*Draba fladnizensis* Wulf.)

Hultén (1968a) shows a station for this species near Savoonga. See *D. lactea*.

128. **Draba alpina** L.

Found at a few scattered stations in barren alpine areas. Common only in glacial cirques near Boxer Bay. The specimens treated here as *D. alpina* are low-grown and

delicate; the siliques are glabrous or with a few simple hairs on the margin. The flowers are brilliant sulphur yellow.

SPECIMENS EXAMINED: *Young 205*, Atuk Mtn.; *1322*, Boxer Bay; *1414*, Murphy River. May also have been collected by Chamisso and Eschscholtz (Hultén 1945). Range: circumpolar, zone 1.

129. **Draba macrocarpa** Adams (*D. Bellii* Holm.)

Found at a single large station in barren hills near Boxer Bay. Differs from *D. alpina*, to which it is closely related, in its slightly more robust growth habit and pubescent siliques.

SPECIMENS EXAMINED: *Young 1323*, Boxer Bay. No previous reports. Range: essentially circumpolar, zone 1.

130. **Draba hirta** L. (*D. glabella* Pursh.)

Common near old village sites near Gambell, one station also found on a rocky stream bank on the south side of the island. Similar to *D. borealis*, but usually larger, more robust, and with only stellate tricomes on the flowering stems.

SPECIMENS EXAMINED: *Young 1377*, Gaedtuk; *1451*, Gambell. Also reportedly collected at Gambell by Chambers (Hultén 1945). Range: circumpolar, arctic; south in central Asia and eastern North America. Northern limit: northern zone 3.

131. **Draba borealis** DC.

Fairly common on backshores and dry tundra at low elevations. There is much variation between specimens, particularly in flower color (which may range from white to pale yellow), growth habit, number of cauline leaves and form of the leaves. The species is closely related to *D. hirta;* it is of somewhat more delicate growth habit, has long simple or forked hairs as well as stellate hairs on the flowering stems, and appears to flower considerably later than *D. hirta,* but intermediates occur for most of these characters. Few of the specimens from St. Lawrence have mature siliques, and none are twisted, a character which Hultén (1945) considers to be characteristic of this species.

SPECIMENS EXAMINED: *Young* 5, Gambell; *428*, Kialegak; *499x*, Siknik; *595*, *654*, *1320*, Boxer Bay; *1420*, Booshu Camp. Also reportedly collected by Chamisso and Eschscholtz (Hultén 1945). Range: amphi-Beringean, mainly near the coasts of the Bering and Okhotsk Seas. Northern limit: unclear because of limited range.

132. **Braya humilis** (C. A. Mey.) Robins.

A single station was found in an area somewhat transitional between dry tundra and fell-field. The specimens have comparatively large flowers and siliques. over 1 mm broad; according to Böcher (1956) they would key to ssp. *arctica* (Böcher) Rollins. This identification is tentative, however, until the cytotaxonomy of this complex group can be worked out in greater detail (cf., Abbe, 1948; Rollins. 1953).

SPECIMENS EXAMINED: *Young 272*, Fossil River. No previous reports. Range: not clear because of taxonomic difficulties. The complex is circumpolar, but it reaches the arctic only in the Western Hemisphere, as far north as the north coast of Greenland.

133. **Parrya nudicaulis** (L.) Regel

Fairly common in alpine seepage areas and snow flushes.

SPECIMENS EXAMINED: *Young 29*, Tapphook; *363*, Kialegak; *683*, *715*, Boxer Bay. Numerous other reports. Range: from Spitzbergen across arctic and central Asia to Alaska and westernmost Canada. Northern limit: zone 2, reaching zone 1 in Severnaya Zemlya.

CRASSULACEAE

134. **Sedum rosea** (L.) Scop.

Common in most habitats except wet tundra and rock deserts. Often abundant on bird cliffs and village sites. Exceptionally robust specimens often occur on decomposed lava. Saint Lawrence specimens are all purple flowered and belong to ssp. *integrifolium* (Raf.) Hult.

SPECIMENS EXAMINED: *Young 76*, Tapphook; *165*, Savoonga; *340*, Northeast Cape; *360*, Kialegak; *520*, Siknik; *618*, Boxer Bay. Numerous other reports. Range: the

entire *S. rosea* complex is nearly circumpolar, but it is absent from the central Canadian Arctic. Disjunct populations occur in many temperate areas. Subspecies *integrifolium* occurs mainly in eastern Asia and western North America. Northern limit: zone 3.

SAXIFRAGACEAE

135. **Saxifraga oppositifolia L.**

Rare; two stations found on talus slopes in glacial cirques near Boxer Bay.

SPECIMENS EXAMINED: *Young 1312*, Boxer Bay. No previous reports. Range: circumpolar, arctic south in alpine regions. Northern limit: zone 1.

136. **Saxifraga Eschscholtzii** Sternb.

Found at two stations on rocky outcrops at low elevations.

SPECIMENS EXAMINED: *Young 1442*, Ataakas Camp. *Geist*, 1933, Poovookpuk (University of Alaska). Range: Beringean and Alaskan endemic. Northern limit not clear because of limited range.

(*Saxifraga serphyllifolia* Pursh)

Reportedly collected by Chamisso (Hultén 1945), but Hultén (*loc. cit.*) suggests that this report may refer to St. Lawrence Bay, on the Chuckhi Peninsula. No modern specimens from St. Lawrence Island are known.

137. **Saxifraga hirculus** L.

Scattered but locally abundant, particularly near Boxer Bay. Occurs on wet tundra, alpine seepage areas, and on gravel banks of rivers.

SPECIMENS EXAMINED: *Young 75*, Tapphook; *222*, Savoonga; *429*, Kialegak; *636*, Boxer Bay; *774*, Gambell. *Mason 6092*. *Geist*, 1933, Southwest Cape. Several other reports. Range: circumpolar, arctic-alpine. Northern limit: zone 1.

138. **Saxifraga flagellaris** Willd.

A few stations were found at fairly low elevations on then North slope of the Kookooligit Range, one on a backshore near Invut Mountain. The specimens have comparatively narrow sepals and few, light colored, stalked glands. They belong to ssp. *flagellaris* according to Porsild's (1954) treatment, but the difference between these specimens and those from eastern Canada is not obvious.

SPECIMENS EXAMINED: *Young 466*, Invut Mtn.; *1425*, Ataakas Camp. Also reportedly collected by Geist (Hultén 1945). Range: circumpolar, arctic. Northern limit: zone 1.

139. **Saxifraga bronchialis** L.

Scattered on rocky outcrops at lower elevations, rare on backshores. There is some variation in the specimens listed, but all apparently belong to ssp. *Funstonii* (Small) Hult.

SPECIMENS EXAMINED: *Young 199*, *206*, Savoonga; *499*, Siknik; *560*, Gaedtuk; *710*, Boxer Bay. *Geist*, 1931, Savoonga; 1933, Boxer Bay. Range: eastern Asia, western North America south in Rocky Mountains. Northern limit: reaches zone 2.

140. **Saxifraga punctata** L.

Common to abundant in practically every terrestrial habitat on St. Lawrence with the exception of foreshores. The material shows a great deal of variation, particularly in the size of the plant, pigmentation, and pubescence. Inflorescences vary from congested heads or spikes to racemes with long capillary branches. If only a few specimens were available from the island, it would be tempting to describe two or more species, but the specimens available seem to cover the total range of variation.

SPECIMENS EXAMINED: *Young 7*, Gambell; *19*, Tapphook; *174*, *179*, *180*, *181*, Savoonga; *292*, *349*, Northeast Cape; *368*, *401*, Kialegak; *515*, Siknik; *630*, Boxer Bay. Numerous other reports. Range: eastern Asia and western North America. Northern limit: zone 2.

141. **Saxifraga spicata** D. Don

A single station was found along the shores of a cave-in lake near Kialegak. Specimens are less high grown than those from central Alaska, but otherwise appear to be similar.

SPECIMENS EXAMINED: *Young 438*, Kialegak. Also reportedly collected by Haley; Hultén (1945) doubts this report. Range: endemic to the Yukon River drainage and Bering Sea coast of Alaska. Northern limit not clear because of limited range.

142. Saxifraga cernua L.

Common on backshores, village sites and hummocks of wet tundra.

SPECIMENS EXAMINED: *Young 156*, Savoonga; *405*, Kialegak; *470*, Siknik; *635*, Boxer Bay; *745*, Gambell. Several other reports. Range: circumpolar, arctic-alpine. Northern limit: zone 1.

(*Saxifraga exilis* Steph.)

Hultén (1968a) indicates on a dot map that this species is known to occur on St. Lawrence. I have no information on these collections. Some of the specimens treated here under *S. cernua* or *S. rivularis* might be considered to be *S. exilis*.

143. Saxifraga nudicaulis D. Don

Abundant on wet tundra, wet alpine areas.

SPECIMENS EXAMINED: *Young 60, 116*, Tapphook; *338*, Northeast Cape; *612*, Boxer Bay. Numerous other reports. Range: endemic to the Bering Strait Region and the shores of the Okhotsk Sea. Northern limit unclear because of restricted range.

144. Saxifraga bracteata D. Don

Typical specimens were found only once, on an old village site near Savoonga. This species is rather doubtfully distinct from *S. rivularis*, particularly where the two are sympatric. Some of the specimens treated here as *S. rivularis* might be identified as *S. bracteata*.

SPECIMENS EXAMINED: *Young 170*, Savoonga. Several other reports. Range: coastal areas near the Bering and Okhotsk Seas. Northern limit unclear because of restricted range.

145. Saxifraga rivularis L.

Common in alpine areas, sea cliffs, village sites, and wet areas in backshores. Apparently somewhat nitrophilous. Specimens from alpine areas are often delicate, strongly pigmented, and erect in growth habit. Those from other areas are weakly pigmented, lax, and tend to approach or merge with *S. bracteata*.

SPECIMENS EXAMINED: *Young 25*, Tapphook; *351*, Northeast Cape; *472*, Siknik; *724, 1413*, Boxer Bay; *776*, Gambell. Several other reports. Range: circumpolar, arctic and a few alpine areas. Northern limit: zone 1.

146. Saxifraga davurica Willd.

Found at a few stations in the Kookooligit Mountains. Specimens are highly variable and show nearly the complete range of variation between *S. davurica, sensu stricto*, and typical *S. unalaschcensis* Sternb., under which name earlier specimens of this group from St. Lawrence have been treated (Hultén 1945, 1968a). There is no indication that more than one population exists on St. Lawrence, and the specimens are best identified as *S. davurica* ssp. *grandipetala* (Engl. and Irmsch.) Hult. The intermediate nature of these specimens suggests that the status of *S. unalaschcensis* as a full species should be reevaluated.

SPECIMENS EXAMINED: *Young 204*, Savoonga; *1441*, Ataakas Camp. *Geist*, 1933. Range: eastern Asia and Alaska-Yukon; *S. unalaschcensis* replaces *S. davurica* in the southern Bering Sea, and the closely related *S. Lyallii* Engler occurs in southern Alaska-Yukon.

(*Saxifraga nivalis* L.)

Reportedly collected at Gambell by Chambers (Hultén 1945). Small specimens of *S. foliolosa* are easily confused with this species. Since I have never found *S. nivalis* on St. Lawrence and have seen no specimens, I exclude it from the flora. However, it is a common high arctic species which should be looked for on the island.

(*Saxifraga unalaschcensis* Sternb.)

See *S. davurica*.

147. **Saxifraga hieracifolia** Waldst. and Kit.

Common on hummocks of wet tundra, on backshores, and in wet alpine areas.

SPECIMENS EXAMINED: *Young 46, 61,* Tapphook; *151,* Savoonga; 295, Northeast Cape; *402,* Kialegak; *609,* Boxer Bay. *Anderson* 3695, Savoonga. Several other reports. Range: circumpolar although somewhat disrupted in Canada and Greenland. Northern limit: zone 2.

148. **Saxifraga foliolosa** R. Br.

Common on hummocks of wet tundra, backshores and in alpine areas. On St. Lawrence, the inflorescence consists mainly of bulblets; flowers are rare.

SPECIMENS EXAMINED: *Young 114,* Tapphook; *174, 242,* Savoonga; 334, Northeast Cape; *471,* Siknik; 655, Boxer Bay; 757, Gambell; *1441,* Ataakas Camp. Several other reports. Range: circumpolar arctic, with a few alpine stations. Northern limit: zone 2, reaches zone 1 in Franz Josef Land.

149. **Chrysosplenium tetrandrum** (Lund) Th. Fries

Common in old village sites, wet spots on backshores, and at the edges of permanent snow patches, where it may be found flowering in late August. Apparently somewhat nitrophilous.

SPECIMENS EXAMINED: *Young 18,* Tapphok; *234,* Savoonga; *430,* Kialegak; *479,* Siknik; *796,* Gambell. Several other reports. Range: circumpolar, but rare in Greenland and northeastern Canada; arctic. Northern limit: zone 2.

150. **Chrysosplenium Wrightii** Franch. and Sav.

On St. Lawrence this species is found only in alpine areas with soil of decomposed lava. It is apparently a calcophile. Abundant in some areas of the Kookooligit Range.

SPECIMENS EXAMINED: *Young 202,* Atuk Mtn.; *1447,* Kangee. Also reportedly collected by Mason (Hultén 1945). Range: Beringean endemic, known only from easternmost Siberia and Alaska-Yukon. Northern limit: unclear because of restricted range, but reaches zone 2 at Wrangel Island.

151. **Parnassia Kotzebuei** Cham. and Schlecht.

Uncommon, usually found in gravel bars, occasional in lower alpine areas.

SPECIMENS EXAMINED: *Young 218,* Savoonga; *407,* Kialegak; *717,* Boxer Bay; *1357,* Gaedtuk; *1437,* Ataakas Camp. Also reported by Anderson (Hultén 1945). Range: arctic-alpine North America and easternmost Siberia. Northern limit: reaches the southern edge of zone 3.

ROSACEAE

(*Spiraea Beauverdiana* Schneider)

Collected by Chamisso according to Kotzebue (Hultén 1945). This is almost certainly a mistake.

152. **Rubus chamaemorus** L.

Fairly common on hummocks in wet tundra areas, but never abundant, as it is on the Alaskan mainland. The natives claim that a good crop of berries occurs only every four to five years.

SPECIMENS EXAMINED: *Young 71,* Tapphook; *160,* Savoonga; 303, Northeast Cape; 524, Siknik; 598, Boxer Bay; 779, Gambell. Several other reports. Range: essentially circumpolar, but rare or absent in most of Greenland and northeastern Canada. Northern limit: northern zone 3.

153. **Rubus arcticus** L.

Common to abundant in mesic tundra, particularly along deeply thawed streambanks on the south side of the island. Elsewhere, this species is rare or absent, with a few stations being found in protected gullies and on raised beaches and other mesic tunda situations. Hultén (1968b) has recently united *R. stellatus* and *R. acaulis* with *R. arcticus,* according each of the last two taxa subspecific rank. On St. Lawrence, single stations of *R. arcticus* (which are probably often single clones, since the underground stolons ramify widely) show a range of variation from the typical lobate

leaves of ssp. *stellatus* to the trifoliolate leaves of ssp. *arcticus*. In most cases, specimens with trilobate leaves are found in more exposed situations near the tops of stream banks and gullies, while trifoliolate specimens occur near the lower edges of the colonies. There is much variation in the glands of the sepals. Some specimens have thin, eglandular sepals, while others are densely glandular. There seems to be no correlation of this character with leaf form or other characters. Petals are usually long and narrow, as in ssp. *stellatus*, but individual specimens may have short, broad petals. I see no evidence that two taxa of *R. arcticus* occur on St. Lawrence. It appears that, at least in the Bering Sea region, *R. arcticus* is more variable than has previously been believed, and it is not possible to decide which of Hultén's (1968b) subspecies is represented in the area.

It is interesting to note that, although *R. arcticus* flowers abundantly on St. Lawrence, I never found a single fruit. The summer of 1967 was unusually mild, and during that time, *R. chamaemorus* set fruit abundantly. It appears that on St. Lawrence, *R. arcticus* is a marginal species which is not able to complete its sexual reproductive cycle under normal climatic conditions, although it is able to spread vegetatively. Some of the larger colonies of *R. arcticus* are probably single clones of great age.

SPECIMENS EXAMINED: *Young 330*, Northeast Cape; *579*, Gaedtuk; *713*, Boxer Bay; *1301, 1302*, Gambell. No previous reports. Range: nearly circumpolar, not known to occur in Greenland or northeastern Canada. Northern limit: reaches the northern edge of zone 4.

154. **Potentilla palustris** (L.) Scop.

Abundant along the shores of Koozaata River, where it was often observed in flower. Otherwise occasional in small ponds, where flowering specimens were seldom observed.

SPECIMENS EXAMINED: *Young 289*, Savoonga; *325*, Northeast Cape; *435*, Kialegak; *660*, Boxer Bay. Several other reports. Range: circumpolar, arctic south to temperate regions. Northern limit: reaches about to the boundary of zone 4-zone 3, with a few stations in zone 3.

(*Potentilla biflora* Willd. ex Schlecht.)

Reportedly collected by Chamisso. Hultén (1946) considers this report doubtful. As there are no specimens of this species known from St. Lawrence, it is excluded from the flora.

155. **Potentilla elegans** Cham. and Schlecht.

Rather common on rock deserts near Boxer Bay; not found elsewhere.

SPECIMENS EXAMINED: *Young 692*, Boxer Bay. No previous reports. Range: scattered stations in the mountains of eastern Siberia and Alaska-Yukon. Northern limit: not clear because of limited range, but reaches zone 2 at Wrangel Island.

156. **Potentilla villosa** Pall. ex Pursh.

Two collections from rocky alpine areas appear to be this species. The situation with respect to the ternate-leaved species of *Potentilla* in arctic Alaska is so confusing and so poorly understood that a meaningful treatment of the specimens from St. Lawrence is tentative. A full monographic study of the group is badly needed. The specimens here treated as *P. villosa* are unusually low-grown, and the flowers are smaller than is usual in this species.

SPECIMENS EXAMINED: *Young 385*, Kialegak; *691*, Boxer Bay. Also reportedly collected by Chamisso and by Geist (Hultén 1946). Range: shores of Bering Sea and southern Alaska and British Columbia. Northern limit: not clear because of limited range.

157. **Potentilla uniflora** Ledeb.

A single collection from a rocky alpine situation is best identified as this species.

SPECIMENS EXAMINED: *Young 573*, Gaedtuk. No previous reports, although Hultén (1968a) shows a station on St. Lawrence. Range: broadly amphi-Beringean, with scattered disjunct stations. Northern limit: zone 3 or southern zone 2.

158. **Potentilla hyparctica** Malte

The specimens treated here as this species form a reasonably homogeneous group of plants which are of rather erect growth habit, and have hirsute, not tomentose, leaves. This is the commonest *Potentilla* on St. Lawrence. It is found mainly on rock deserts, dry stream banks, and occasionally on backshores, where it may be rather low-grown.

SPECIMENS EXAMINED: *Young 8*, Gambell; *51*, Tapphook; *190*, Savoonga; *384*, Kialegak; *478*, *521*, Siknik; *716*, *1315*, Boxer Bay; *1407*, Southwest Cape; *1449*, Savoonga. Several other reports are probably referable to this species. Range: circumpolar, arctic. Northern limit: zone 1.

(*Potentilla Hookeriana* Lehm.)

Hultén (1968a) indicates on a dot map that this species occurs on St. Lawrence Island. I have not seen a specimen from the island which could be referred to this species.

159. **Potentilla Egedii** Wormsk.

Common along the banks of the Koozaata River near Nuna; otherwise only a few small specimens found in brackish coastal areas.

SPECIMENS EXAMINED: *Young 144*, Tapphook; *464*, Kialegak; *518*, Siknik. No previous reports, but the species is shown by Hultén (1968a) as occurring on the island. Range: essentially circumpolar, but disrupted. Gaps in Siberia, as in the case of many coastal species. Northern limit: barely reaches the lower edge of zone 3.

160. **Geum glaciale** Adams

Fairly common in high alpine areas in the Kookooligit and Poovoot Ranges.

SPECIMENS EXAMINED: *Young 193*, Atuk Mtn.; *1327*, Boxer Bay. *Geist*, 1933, Boxer Bay (University of Alaska). Range: arctic Siberia and Alaska-Yukon. Northern limit: zone 2.

161. **Dryas octopetala** L.

Fairly common on rocky alpine areas, usually at rather low elevations. According to the treatment of Juzepczuk (1929) and Porsild (1947), three different species might be distinguished in St. Lawrence Island material of this species. Hultén (1968a) treats all of the older specimens from St. Lawrence as ssp. *octopetala*, but to me most specimens seem to be more closely allied to ssp. *punctata* (Juz.) Hult. There is no evidence that more than one species of this group is represented on the island, and much of the material can hardly be equated with any of the species proposed by Porsild (*loc. cit.*).

SPECIMENS EXAMINED: *Young* 35, Tapphook; *182*, Savoonga; *381*, Kialegak; *708*, Boxer Bay; *770*, Gambell; *1361*, Gaedtuk; *1445*, Kangee. Several other reports. Range: essentially circumpolar, but rare in arctic Canada, where it is replaced by *D. integrifolia*. Northern limit: zone 2, reaching zone 1 in the vicinity of Taimayr Peninsula.

162. **Dryas integrifolia** M. Vahl

A single station found along the shores of a cave-in lake near Kialegak.

SPECIMENS EXAMINED: *Young 440*, Kialegak. This is undoubtably the same station as that found by Chamisso and Eschscholtz (Hultén 1946). Range: arctic-alpine. Almost entirely confined to North America. Northern limit: northern boundary of zone 2.

LEGUMINOSAE

163. **Astragalus umbellatus** Bunge

Uncommon, usually found on alpine seepage areas.

SPECIMENS EXAMINED: *Young* 92, Tapphook; *707*, Boxer Bay. *Mason 6113*, Aivichtook Lagoon. Also reportedly collected by Geist (Hultén 1946). Range: arctic Siberia and Alaska-Yukon, with a few outlying stations. Northern limit: zone 2.

164. **Astragalus alpinus** L.

Reportedly collected by Mason (Hultén 1947). There is no reason to doubt the authenticity of this report, but I have never collected this species on St. Lawrence. It must be of rare and local occurrence.

SPECIMENS EXAMINED: none. Range: arctic-alpine; nearly circumpolar, but rare or absent in Greenland, Spitzbergen and northeastern Canada. Northern limit: zone 2.

165. **Oxytropis Maydelliana** Trautv.

Of scattered occurrence on rocky areas around the periphery of the Kookooligit Range.

SPECIMENS EXAMINED: *Young 1360*, Gaedtuk. Also reportedly collected by Mason and by Geist (Hultén 1946). Range: arctic North America and easternmost Siberia. Northern limit: zone 2.

166. **Oxytropis nigrescens** (Pall.) Fisch.

Fairly common, particularly on fell-fields. The most common form is ssp. *bryophila* (Greene) Hult., but in the higher mountains, the dwarf ssp. *pygmaea* (Pall.) Hult. may be found growing with the larger form. There is some evidence of intergradiation, but the two forms generally remain distinct.

SPECIMENS EXAMINED: (ssp. *bryophila*) *Young 101*, Kookooliktook River; *191*, Savoonga; *297*, Fossil River; *374*, Kialegak (ssp. *pygmaea*). *Geist*, 1933, Boxer Bay. *Mason*, July 10, 1931, Aivichtook Lagoon. Several other reports. Range: eastern Siberia and Alaska-Yukon. Northern limit zone 3, reaches zone 2 at Wrangel Island.

167. **Hedysarum alpinum** L.

Uncommon on drier alpine areas at low elevation.

SPECIMENS EXAMINED: *Young 88*, Tapphook; *556*, *1376*, Gaedtuk. Also reported by Kjellman (1882) under *H. obscurum*. Range: several large disjunct areas in Siberia and North America. Mainly an alpine species, but reaching the arctic in several areas. Northern limit; not clear, but reaches zone 3 in several places.

168. **Lathyrus japonicus** Willd. (*L. maritimus* L.)

Occasional in the *Elymus* zone on foreshores. Specimens from St. Lawrence are all pubescent. They apparently belong to var. *aleuticus* (Greene) Fern., although there is some question as to whether this is the same taxonomic unit in the Bering Sea region as in the Atlantic region. Two taxa may be involved.

SPECIMENS EXAMINED: *Young 131*, Tapphook; *457*, Kialegak; *546*, Barrier Beach of Koozaata Lagoon. *Geist*, 1933, "western half." Range: essentially circumpolar but, as with other strand species, having large gaps in Canada and Siberia. Northern limit: in Beringean region reaches zone 2 at Wrangel Island. In Atlantic region reaches only to southern zone 4.

CALLITRICHACEAE

169. **Callitriche verna** L.

Abundant in a couple of small ponds near Savoonga; not known from elsewhere on the island. The specimens have sessile, wingless fruits with no visible styles.

SPECIMENS EXAMINED: *Young 1421*, Savoonga. No previous reports. Range: not entirely clear because of taxonomic problems, but apparently circumpolar in boreal and temperate regions and in the southern part of the southern hemisphere. Northern limit: zone 4, reaching zone 3 in east and west Greenland as well as St. Lawrence.

VIOLACEAE

170. **Viola biflora** L.

A few stations found near snow patches near Gaedtuk.

SPECIMENS EXAMINED: *Young 552*, Gaedtuk. *Geist*, 1933, "Noong Woak's Camp." Range: disjunct in arctic and alpine regions of Eurasia and western North America. Northern limit: northern zone 4.

171. **Viola epipsila** Ledeb.

Rare on mesic tundra. The St. Lawrence specimens belong to the slightly differentiated form sometimes known as *V. achyrophora* Greene.

SPECIMENS EXAMINED: *Young 134,* Tapphook; 253, Savoonga. Also reportedly collected by Anderson, Mason (Hultén 1946). Range: nearly circumpolar, but not known to occur in Greenland and eastern Canada. Northern limit: zone 4.

ONAGRACEAE

172. **Epilobium angustifolium** L.

A few small stations found on coastal areas around the periphery of the island. All specimens were sterile. The individual stations are probably clones developed from seeds dispersed from the Siberian or Alaskan mainland.

SPECIMENS EXAMINED: *Young 790,* Gambell. No previous reports. Range: circumpolar, arctic, boreal, and temperate regions. Northern limit: reaches about to the boundary between zone 4 and zone 3.

173. **Epilobium latifolium** L.

Common to abundant in gravelly stream beds, rare or absent in other habitats.

SPECIMENS EXAMINED: *Young 93,* Kookooliktook River; 239, Savoonga. Also reportedly collected by Geist (Hultén 1946). Range: circumpolar, arctic-alpine. Northern limit: zone 2.

174. **Epilobium palustre** L.

Rare; found growing with *E. anagallidifolium* along a few stream banks on the south side of the island.

SPECIMENS EXAMINED: *Young 1362, 1386,* Gaedtuk. No previous reports. Range: circumpolar, arctic to temperate regions. Northern limit: northern edge of zone 4, reaching zone 3 in St. Lawrence and in East Greenland.

175. **Epilobium anagallidifolium** Lam.

Common to abundant on mesic tundra along stream banks on the south side of the island; rare or absent elsewhere. The distribution on St. Lawrence is similar to that that of *Rubus arcticus*.

SPECIMENS EXAMINED: *Young 742, 1303,* Gambell; *1352,* Gaedtuk. No previous reports. Range: arctic-alpine; circumpolar but fragmented, with several large gaps. Northern limit: northern zone 4, reaching zone 3 in several areas.

HALORAGACEAE

176. **Hippuris vulgaris** L.

Fairly common in small tundra and backshore pools. In some sheltered spots, specimens approach *H. tetraphylla* L.

SPECIMENS EXAMINED: *Young 248,* Savoonga; *324,* Northeast Cape; *403,* Kialegak; *517,* Siknik; *747,* Gambell. Several other reports. Range: circumpolar, arctic south to temperate regions. Northern limit: northern zone 3, with some zone 2 stations. (*Hippurus tetraphylla* L.)

Hultén (1968a) locates a station for this species on St. Lawrence. Individual specimens of *H. vulgaris* may approach this species.

UMBELLIFERAE

177. **Ligusticum mutellinoides** (Crantz) Willar

Occasional in rocky alpine areas and fell-fields.

SPECIMENS EXAMINED: *Young 100,* Tapphook; *273,* Fossil River; *570,* Gaedtuk; *700,* Boxer Bay. No previous reports, but Hultén (1968a) locates a station for this species on St. Lawrence. Range: several disjunct areas in Eurasia and Alaska, arctic-alpine. Northern limit: not clear; reaches zone 3 in St. Lawrence and Novaya Zemlya.

178. **Conioselinum chinense** (L.) BSP.

Occasional on barrier beaches on the south side of the island. The entire plant is seldom over 10 cm tall, and the inflorescence is sometimes hardly raised above the surface of the sand.

SPECIMENS EXAMINED: *Young 425*, Kialegak; *483*, Siknik; *651*, Boxer Bay. *Geist*, 1934, Punuk Islands. No other reports. Range: not entirely clear because of taxonomic difficulties. Apparently found in temperate eastern North America and along the north Pacific and Bering Sea coasts of Asia and America. Reaches the arctic only in the vicinity of Bering Strait.

179. **Angelica lucida** L.

Fairly common on barrier beaches on the southern part of the island. Also found in the mountains near Boxer Bay.

SPECIMENS EXAMINED: *Young 82*, Tapphook; *376*, Kialegak; *687*, Boxer Bay. Also reported by Kjellman (1882). Range: not entirely clear because of taxonomic questions, but apparently nearly identical to that of *Conioselinum chinense*. The ranges of these two Umbelliferous species are unique.

CORNACEAE

180. **Cornus suecica** L.

Occasional on mesic tundra. Usually found in large, isolated patches which may be individual clones.

SPECIMENS EXAMINED: *Young 77*, Tapphook; *320*, Northeast Cape; *388*, Kialegak; *554*, Gaedtuk; *772*, Gambell. Several other reports. Range: both amphi-Beringean and amphi-Atlantic, mainly near the coast. Northern limit: northern zone 4.

PYROLACEAE

181. **Pyrola grandiflora** Radius

A single specimen was found in an alpine area near Kialegak.

SPECIMEN EXAMINED: *Young* 393, Kialegak. Also reported by Kjellman (1882). Range: circumpolar, arctic-alpine. Northern limit: northern zone 3.

EMPETRACEAE

182. **Empetrum nigrum** L.

Of scattered occurrence on some backshore and fell-field areas. Never abundant, as on the mainland of Alaska, and seldom if ever sets an abundant crop of fruit. All specimens have bisexual flowers [*E. hermaphroditum* (Lge.) Hagerup].

SPECIMENS EXAMINED: *Young 34*, Tapphook; *220*, Savoonga; *300*, Northeast Cape; *396*, Kialegak; *506* Siknik; *627*, Boxer Bay; *766*, Gambell. Several other reports. Range: circumpolar, arctic-alpine. Northern limit: northern edge of zone 3.

ERICACEAE

183. **Ledum decumbens** (Ait.) Lodd.

Occasional on fell-fields, boulder slopes, and hummocks of wet tundra.

SPECIMENS EXAMINED: *Young 99*, Tapphook; *302*, Northeast Cape; 382, Kialegak; *559*, Gaedtuk; *761*, Gambell. Several other reports. Range: circumpolar, arctic. Northern limit: zone 3.

184. **Loiseleuria procumbens** (L.) Desv.

Occasional on fell-fields, alpine tundra.

SPECIMENS EXAMINED: *Young 102*, Tapphook; 339, Northeast Cape; *391*, Kialegak. Also reportedly collected by Chambers (Hultén 1947). Range: essentially circumpolar, arctic-alpine. Northern limit: zone 3.

185. **Phyllodoce coerulea** (L.) Bab.

Common to abundant in one small area on the north slope of the Kookooligit Range. Otherwise unknown from the island. The flowers of these specimens are bright carmine red, fading to deep purple when dried. Otherwise they appear to be indistinguishable from specimens from other parts of the arctic.

SPECIMENS EXAMINED: *Young 175*, Kookooligit Mtns. No previous reports. Range: circumpolar, but somewhat disrupted; arctic-alpine. Northern limit: zone 3.

186. **Cassiope tetragora** (L.) D. Don

Common, sometimes abundant on most rocky alpine areas.

SPECIMENS EXAMINED: *Young* 37, Tapphook; *189*, Savoonga; *297*, Northeast Cape; 359, Kialegak; *600*, Boxer Bay. Several other reports. Range: circumpolar, arctic. Northern limit: zone 2, the only ericaceous species found widely in zone 2.

187. **Andromeda polifolia** L.

Common on wet tundra at one small area near Northeast Cape, otherwise rare or absent. Both Kjellman (1882) and Muir (1918) claim that this species is common on the northwestern portion of the island, probably near Gambell. I have not found it there.

SPECIMENS EXAMINED: *Young 326*, Northeast Cape. Also collected by Kjellman. Range: circumpolar, arctic and boreal regions. Northern limit: reaches to the northern edge of zone 4.

188. **Arctostaphylos alpina** (L.) Spreng.

Scattered on lower alpine slopes, particularly in moist boulder talus.

SPECIMENS EXAMINED: *Young* 38, Tapphook; 329, Northeast Cape; *762*, Gambell. Several other reports. Range: circumpolar, arctic-alpine. Northern limit: northern zone 3.

189. **Vaccinium uliginosum** L.

Two small stations found on dry tundra. No flowering or fruiting specimens were observed.

SPECIMENS EXAMINED: *Young 262*, Ataakas Camp; 367, Kialegak. No previous reports. Range: circumpolar, arctic and boreal regions. Northern limit: reaches northern zone 4 in most areas, but to northern zone 3 or even zone 2 in Canada and Greenland. This is apparently correlated with the complex taxonomy of the group, which is being treated in a separate paper (Young, in press).

190. **Vaccinium vitis-idaea** L.

Scattered on hummocks of wet tundra. Most specimens are dwarfed, have few flowers, and do not set fruit heavily.

SPECIMENS EXAMINED: *Young* 52, Tapphook; 264, Savoonga; *305*, Northeast Cape; *390*, Kialegak; *765*, Gambell. Several other reports. Range: essentially circumpolar, arctic and boreal regions. Northern limit: northern zone 3, with a few stations in zone 2.

DIAPENSIACEAE

191. **Diapensia lapponica** L.

Common on exposed rocky alpine areas.

SPECIMENS EXAMINED: *Young 36*, Tapphook; *294*, Northeast Cape; *684*, Boxer Bay. Several other reports. Range: essentially circumpolar, somewhat disrupted; arctic alpine. Northern limit: zone 3.

PRIMULACEAE

192. **Primula nivalis** Pall.

The specimens treated here as *P. nivalis* and *P. tschuktschorum* form a small but extremely difficult group about which no two authors seem to agree. The recent treatments of Porsild (1965) and Hultén (1968a) place all Alaskan specimens of

section *Nivales* of the genus *Primula* in *P. tschuktschorum*. Having observed members of this group under field conditions on St. Lawrence Island and the Alaskan mainland, I conclude that there are two species present in western Alaska, that there is probably some intergradation between the species, and that each species shows a considerable amount of variation, most of which is so random that it makes it difficult to delineate subspecific taxa. A final understanding of the group must wait until an intensive biosystematic study has been made.

Hultén (1948) considers that the major difference between *Primula tschuktschorum* and *P. nivalis* is the presence or absence of a scaly leafless sheath surrounding the base of the plant. This sheath is actually formed by the bladeless petioles of basal leaves, and it serves as a protective covering for the overwintering buds. In specimens that are here considered to be typical *P. tschuktschorum*, these scales are heavily farinose and short and broad, with no rudiments of leaf blades. In the specimens placed in *P. nivalis*, the scales are narrow, effarinose, and usually develop at least rudimentary leaf blades. Therefore, specimens collected at the time of flowering do not appear to have a basal sheath. These specimens normally have narrow, ligulate leaves which are usually ascending, and they often have margins denticulate nearly to the base. The entire plant is effarinose, except occasionally the inner surfaces of the sepals are farinose. Specimens of this type are normally found on dry tundra, rocky outcrops, or dry stream banks.

Specimens here placed in *Primula tschuktschorum* have broad, lax leaves, with only a few faint, widely spaced denticulations near the apex. Typical specimens are somewhat farinose; the basal sheath is always heavily farinose. The plants are normally more robust than those placed in *P. nivalis*, and the inflorescence often contains 20 or more flowers. Specimens of this type are found on backshores, near old village sites, and in wet alpine areas near permanent snow patches. It should be mentioned that a large part of the material studied is somewhat intermediate in one or more of the characters mentioned, probably due to hybridization between the two types.

Porsild (1965) described a new variety of *Primula tschuktschorum*, var. *beringensis* from a single collection made at Boxer Bay by Sauer. In one small seepage area at Boxer Bay, there is a small population of plants which undoubtedly was the source of the specimens discussed by Porsild. These are treated here under *P. nivalis*, although they are not typical specimens of that species. Plants of this type apparently occur only in this one station (less than an acre in extent), and I can see no reason for maintaining a separate variety for them.

SPECIMENS EXAMINED: *Young* 583, Gaedtuk; *610*, Boxer Bay; *803*, Gambell. Range: mountains of eastern Asia, probably reaching Alaska only in the Bering Strait region.

193. **Primula tschuktschorum** Kjellm.

Common in most habitats on St. Lawrence. See *P. nivalis*.

SPECIMENS EXAMINED: *Young* 3, *1457*, Gambell; *47*, *65*, Tapphook; *153*, Savoonga; *348*, Northeast Cape; *456*, Kialegak; *474*, Siknik; *620*, Boxer Bay. Range: Beringean endemic, with a few stations in central Alaska and eastern Siberia. Northern limit: not clear because of limited range.

194. **Primula borealis** Duby

Common to abundant on backshores and lower alpine areas. Many specimens are slightly farinose on the under sides of the leaves, as in var. *ajanensis* (E. Busch.) Hult., but the variation in this character between individuals of the same colony is so great that it cannot have much significance. Some of the larger specimens have a well-developed basal sheath, similar to that found in *P. tschuktschorum*, possibly indicating intergradation between the two species.

SPECIMENS EXAMINED: *Young* 67, Tapphook; *213*, Savoonga; *426*, Kialegak; *477*, Siknik. Many other reports. Range: amphi-Beringean. Northern limit: zone 3.

195. **Douglasia ochotensis** (Willd.) Hult. (*Androsace ochotensis* Willd.)

Common in the central portion of the island, both in alpine areas and on backshores, rare otherwise.

SPECIMENS EXAMINED: *Young* 203, Kookooligit Mtns.; *467*, Invut Mtn.; *531*,

Siknik; *690*, Boxer Bay. Several other reports. Range: amphi-Beringean, mountains of eastern Siberia and Alaska. In central Alaska-Yukon, replaced by *D. arctica* Hook. and *D. Gormani* Constance. Northern limit: not clear because of limited range, but known to occur on Wrangel Island, zone 2.

196. **Androsace chamaejasme** Host

Fairly common on the drier alpine areas, especially at lower elevations.

SPECIMENS EXAMINED: *Young 214, 260*, Savoonga; *488*, Siknik; *677*, Boxer Bay. Several other reports. Range: exceptionally fragmented; occurs in many alpine areas in Eurasia and western North America. Northern limit: not clear, but reaches zone 2 at several stations.

(*Dodecatheon frigidum* Cham. and Schlecht.)

Reportedly collected by Haley (Hultén 1947). The provenience of this specimen is questioned by Hultén (*loc. cit.*) for reasons already mentioned, and no other collectors have found the species on St. Lawrence.

197. **Trientalis europaea** L.

Found growing on hummocks of wet tundra at a single station.

SPECIMENS EXAMINED: *Young 551*, Gaedtuk. No prevous reports. Range: Eurasia and western North America, mainly in boreal regions. Northern limit: lower zone 4, except in the Bering Strait region.

PLUMBAGINACEAE

198. **Armeria maritima** (Mill.) Willd.

Accepted with considerable hesitation as being a member of the St. Lawrence flora. Reportedly collected at Savoonga by Geist (Hultén 1948). There are no other reports, and I was unable to find any specimens. It is possible that Geist's specimen is mislabeled as to location.

SPECIMENS EXAMINED: none. Range: circumpolar, arctic-alpine and boreal regions. Northern limit: northern zone 3, with some zone 2 stations.

GENTIANACEAE

199. **Gentiana algida** Pall.

Fairly common on dry, rocky tundra, particularly on the southern and central parts of the island.

SPECIMENS EXAMINED: *Young 276*, Fossil River; *623*, Boxer Bay. *Geist*, 1933, Poovookpuk; also reported by Kjellman (1882). Range: fragmented; alpine areas of Europe, eastern Eurasia and western North America. Northern limit: not clear, reaches zone 2 in New Siberian Islands.

200. **Gentiana glauca** Pall.

Fairly common on moist tundra, solifluction lobes, and along stream banks.

SPECIMENS EXAMINED: *Young 89*, Tapphook; *245*, Savoonga; *319*, Northeast Cape; *392*, Kialegak; *500*, Siknik; *591, 719*, Boxer Bay; *749*, Gambell. Several other reports. Range: amphi-Beringean. Northern limit: zone 3.

201. **Gentiana auriculata** Pall.

A single station found on a gravel bar near Gaedtuk. The only other Alaskan collection of this species is from Attu Island.

SPECIMENS EXAMINED: *Young 1390*, Gaedtuk. No previous reports. Range: coastal areas of eastern Siberia. Northern limit: not clear because of limited range.

POLEMONIACEAE

202. **Polemonium boreale** Adams

Common on wet tundra, backshores, and lower alpine slopes. In his recent treatment of the North American species of *Polemonium*, Davidson (1950) placed most St. Lawrence specimens in *P. boreale*. Hultén (1948, 1968a), on the other hand,

treats all specimens as *P. acutiflorum* Willd. According to the key given by Davidson (*loc. cit.*) most of the specimens from St. Lawrence that I have examined fall into *P. boreale,* but certain individuals have at least some of the characters of *P. caeruleum* ssp. *villosum* (*P. acutiflorum* of Hultén).

This genus seems to resist all taxonomic attempts to define it. Since I can see no indication whatever that more than one taxon occurs on St. Lawrence. I prefer to treat all specimens under *P. boreale* until such time as the systematics of *Polemonium* in Alaska are correctly presented.

SPECIMENS EXAMINED: *Young 137,* Tapphook; *157,* Savoonga; *299,* Northeast Cape; *409, 424,* Kialegak (*424* is a white flowered form); *519,* Siknik; *622,* Boxer Bay. *Geist,* 1933, Poovookpuk. Several other specimens collected by Chambers are listed by Davidson (1950). Range: nearly circumpolar, but absent in northeastern Canada and western Greenland. Northern limit: zone 2.

BORAGINACEAE

203. **Eritrichium aretioides** (Cham.) D. C.

A single station found in mesic tundra near Boxer Bay. The distinction between this species and *Eritrichium Chamissonis* is not entirely clear. Hultén (1949) claims that the form of the teeth on the nutlets is diagnostic, but this character may be somewhat overemphasized. The single specimen listed here is undoubtably *E. aretioides.* It is loosely cespitose, has comparatively large leaves, and the flowering stems exceed the basal leaves by about 5 cm. Some of the specimens listed under *E. Chamissonis* have somewhat elongated flowering stems, and might be intermediates.

SPECIMENS EXAMINED: *Young 1313,* Boxer Bay. No previous reports. Range: arctic areas in Siberia, arctic-alpine areas in Alaska-Yukon. Northern limit: zone 2, possibly zone 1 in Siberian Islands.

204. **Eritrichium Chamissonis** DC.

Of scattered occurrence on dry, rocky alpine areas and dry tundra.

SPECIMENS EXAMINED: *Young 263, 1430,* Ataakas Camp; *441,* Kialegak. Several other reports. Range: coastal areas in the Beringean region. Northern limit: unclear because of limited range.

205. **Myosotis alpestris** Schmidt

I have never found this species on the island, but it was twice collected by Geist.

SPECIMENS EXAMINED: *Geist,* 1933, Poovookpuk; also reportedly collected by Geist at Atuk Mtn. (Hultén 1949). Range: Eurasia and western North America; arctic-alpine. Northern limit: zone 2.

206. **Mertensia maritima** (L.) S.F. Gray

Fairly common on foreshores, mostly seaward of the *Elymus* zone.

SPECIMENS EXAMINED: *Young 135,* Tapphook; *268,* Savoonga; *343,* Northeast Cape; *459,* Kialegak; *486,* Siknik; *652,* Boxer Bay. Several other reports. Range: similar to other strand plants; circumpolar except for a large gap along the coast of Arctic Siberia. Northern limit: northern zone 3.

[*Mertensia paniculata* (Ait.) D. Don]

Reportedly collected by Chamisso; this report is considered doubtful by Hultén (1949). I concur with this, as no modern specimens exist.

SCROPHULARIACEAE

207. **Lagotis glauca** Gaertn.

Fairly common on wet alpine areas. Most specimens have narrow, sharply denticulated leaves, typical of ssp. *minor* (Willd.) Hult. The distinction between this subspecies and ssp. *glauca* is not clear in St. Lawrence specimens.

SPECIMENS EXAMINED: *Young 43, 110,* Tapphook; *383,* Kialegak; *581,* Gaedtuk, *662,* Boxer Bay; *805,* Gambell. Several other reports. Range: arctic Siberia and Alaska-Yukon. Northern limit: zone 3.

208. **Pedicularis verticillata** L.

Common on backshores, often abundant on old village sites, near bird cliffs.

SPECIMENS EXAMINED: *Young 414,* Kialegak; *1452,* Gambell. Several other reports. Range: Eurasia and Alaska-Yukon; arctic-alpine. Northern limit: zone 3, reaching zone 2 at Wrangel Island.

209. **Pedicularis parviflora** J. E. Smith ssp. *Pennellii* (Hult.) Hult.

Fairly common on hummocks of wet tundra.

SPECIMENS EXAMINED: *Young* 333, Northeast Cape; *616,* Boxer Bay; *755,* Gambell. Several other reports. Range: amphi-Beringean. Northern limit: not clear, probably zone 3.

210. **Pedicularis Langsdorffii** Fisch. (*P. arctica* R. Br.)

Common on moist tundra and alpine areas.

SPECIMENS EXAMINED: *Young 49,* Tapphook; *331,* Northeast Cape; *364,* Kialegak; *498,* Siknik; *631,* Boxer Bay; *801,* Gambell. Several other reports. Range: North America and Siberia; arctic-alpine. Northern limit: zone 2.

211. **Pedicularis sudetica** Willd.

Fairly common on wet and mesic tundra. This is a complex circumpolar group which has recently been monographed by Hultén (1961). Two forms found on St. Lawrence are quite distinct when observed in the field, but the distinctive characters mainly have to do with flower color, and they are not obvious on herbarium specimens. The form treated by Hultén (*loc. cit.*) as ssp. *albolabiata* is robust with large cauline leaves. The lip of the flower is white with deep purple spots, the galea purple. The other form, apparently ssp. *interioroides* Hult., is more delicate in growth habit and has smaller cauline leaves. The entire corolla is bright carmine red. There is little evidence of intergradation between the two forms on St. Lawrence, but intermediates are occasionally found on the Alaskan mainland.

SPECIMENS EXAMINED: (ssp. *albolabiata*) *Young* 433, Kialegak; (ssp. *interiorioides*) *Young* 95, *113,* Tapphook; *196, 255,* Savoonga; 332, Northeast Cape; *411,* Kialegak; 528, Siknik; *613,* Boxer Bay; *758,* Gambell. Several other reports. Range: nearly circumpolar, absent in Greenland; arctic-alpine. Northern limit: zone 2.

212. **Pedicularis capitata** Adams

Fairly common in moist alpine areas, particularly near snow patches.

SPECIMENS EXAMINED: *Young 40,* Tapphook; *177,* Savoonga; *269,* Northeast Cape; 355, Kialegak; *706,* Boxer Bay; *775,* Gambell. Several other reports. Range: North America and Siberia; arctic-alpine. Northern limit: zone 2.

213. **Pedicularis Oederi** M. Vahl

Fairly common along grassy stream banks and in moist alpine situations.

SPECIMENS EXAMINED: *Young 44,* Tapphook; 258, Savoonga; 696, Boxer Bay; 732, Gambell. Several other reports. Range: Eurasia and western North America; arctic-alpine. Northern limit: not entirely clear; apparently reaches some zone 2 areas.

214. **Pedicularis Kanei** Durand (*P. lanata* Willd.)

Common on drier alpine areas, occasional on backshores.

SPECIMENS EXAMINED: *Young* 28, Tapphook; *200,* Savoonga; 285, Northeast Cape; 437, Kialegak; 482, Siknik; 699, Boxer Bay. Several other reports. Range: circumpolar, arctic-alpine. Northern limit: zone 2.

RUBIACEAE

215. **Galium Brandegei** Gray

A single station found at the edge of a muddy, ephemeral pool near Gaedtuk.

SPECIMENS EXAMINED: *Young 1385,* Gaedtuk. No previous reports. Range: alpine and boreal North America. Northern limit: zone 4, with zone 3 stations on St. Lawrence and west Greenland.

CAPRIFOLIACEAE

216. **Linnaea borealis** L.

Two sterile specimens found on moist alpine tundra. Both Kjellman (1882) and Muir (1918) note that this species was common on the northwest portion of the island when they visited there about 1880. It is now rare on all parts of the island.

SPECIMENS EXAMINED: *Young 356,* Kialegak; 553, Gaedtuk. Also collected by Kjellman. Range: circumpolar, arctic and boreal regions. Northern limit: zone 4.

VALERIANACEAE

217. **Valeriana capitata** Pall.

Scattered on backshores and mesic tundra.

SPECIMENS EXAMINED: *Young 61,* Tapphook; *219,* Savoonga; *415,* Kialegak; *510,* Siknik; *676,* Boxer Bay; *744,* Gambell. Several other reports. Range: Siberia and Alaska-Yukon. Northern limit zone 3, with some zone 2 stations.

CAMPANULACEAE

218. **Campanula lasiocarpa** Cham.

Common in a few areas of mesic tundra and along river banks on the south side of the island.

SPECIMENS EXAMINED: *Young 1332,* Boxer Bay. No previous reports. Range: amphi-Beringean. Northern limit: zone 4 except for St. Lawrence.

219. **Campanula uniflora** L.

A single station found in dry, rocky tundra.

SPECIMENS EXAMINED: *Young 586,* Gaedtuk. No previous reports. Range: fragmented, nearly circumpolar, but absent from much of Siberia; arctic-alpine. Northern limit: zone 2.

COMPOSITAE

220. **Solidago multiradiata** Ait.

Occasional, usually found in dry rocky stream beds in the southern and central portions of the island.

SPECIMENS EXAMINED: *Young 387,* Kialegak; *561,* Gaedtuk. *Geist,* 1933, Poovookpuk. Two other collections of Geist listed by Hultén (1950). Range: arctic and boreal regions of North America. Northern limit: southern zone 3.

221. **Aster sibiricus** L.

A single small station found on a gravel river bar. The specimens are exceptionally low-grown and bear only a single head.

SPECIMENS EXAMINED: *Young 1359,* Gaedtuk. No previous reports. Range: northern European USSR, Siberia, and western North America. Northern limit: zone 3.

222. **Antennaria monocephala** DC.

Occasional, usually found on gravel bars along small streams.

SPECIMENS EXAMINED: *Young 183,* Savoonga; *569,* Gaedtuk. Also reportedly collected by Anderson (Hultén 1950). Range: several closely related forms occur in arctic North America and Greenland. Northern limit: southern zone 3.

223. **Chrysanthemum arcticum** L.

Common on both foreshores and backshores, occasional on old village sites.

SPECIMENS EXAMINED: *Young 133, 136,* Tapphook; *314,* Northeast Cape; *412,* Kialegak; *469,* Siknik; *645,* Boxer Bay; *732,* Gambell. Several other reports. Range: several disjunct areas in arctic and boreal regions along the coast of Eurasia and North America. Northern limit: zone 4, with some zone 3 stations.

(*Chrysanthemum integrifolium* Richards.)

Hultén (1950) gives a single report of this species from St. Lawrence, but thinks that the location is incorrect. I have never seen this species on the island.

224. **Artemisia globularia** Cham. ex Besser

Rare, found only in alpine areas near Boxer Bay. This characteristic species does not seem to form hybrids with any others of the *A. arctica* group.

SPECIMENS EXAMINED: *Young 685*, Boxer Bay. Also reportedly collected by Eschscholtz (Hultén 1950). Range: Beringean endemic. Northern limit: not clear because of limited range, but reaches zone 2 at Wrangel Island.

225. **Artemisia glomerata** Ledeb.

Rather common in dry alpine areas in the Poovoot Range and near Ataakas Camp in the Kookooligit Range. Specimens which appear to be intermediates grow in areas where this species is found with *artemisia trifurcata*. Some of the specimens of *A. glomerata* from Ataakas Camp have congested inflorescences with small, nearly sessile heads, and with light colored margins of the involucral bracts. These specimens resemble *A. senjavinensis*, but they have a few hairs on the corolla, and therefore should be excluded from that species. *Artemisia senjavinensis* appears to replace *A. glomerata* in parts of western Alaska. The specimens mentioned above suggest that the distinction between the two species is less firm than has been assumed, and that the two forms might best be considered a single species.

SPECIMENS EXAMINED: *Young 266, 1427, 1433*, Ataakas Camp; *644, 1316, 1333, 1415*, Boxer Bay. *Geist*, 1933, Poovookpuk. Also reportedly collected at Savoonga by Geist (Hultén 1950). Range: amphi-Beringean. Northern limit: not clear, but reaches zone 2 at Wrangel Island.

226. **Artemisia Tilesii** Ledeb.

Common to abundant on backshores, lower alpine areas. Especially abundant on old village sites, where it is usually the dominant species. All specimens appear to belong to the typical arctic form, ssp. *Tilesii*.

SPECIMENS EXAMINED: *Young 80*, Tapphook; *250*, Savoonga; *318*, Northeast Cape; *542*, Siknik; *791*, Gambell. Several other reports. Range: nearly circumpolar, absent in Greenland, eastern Canda and western Europe. Northern limit: lower zone 2.

227. **Artemisia arctica** Less.

Common to abundant on backshores, hummocks of wet tundra, and lower alpine areas. Often abundant on old village sites. There is a great deal of variation within populations of this species on St. Lawrence. Specimens with rust-red pubescence on the spike [ss. *beringensis* (Hult.) Hult.] appear to be randomly distributed within populations of the more common form with yellow pubescence (ssp. *arctica*). Intermediates are also common.

SPECIMENS EXAMINED: *Young 68, 81*, Tapphook; *241*, Savoonga; 322, Northeast Cape; *371*, Kialegak; 543, Siknik; *641*, Boxer Bay; 797, Gambell. Several other reports. Range: eastern Siberia and western North America. Northern limit: zone 3.

228. **Artemisia borealis** Pall.

A single station found in an alpine fell-field near Boxer Bay.

SPECIMENS EXAMINED: *Young* 725, Boxer Bay. No previous reports, but Hultén (1968a) indicates a station on St. Lawrence. Range: nearly circumpolar, absent in East Greenland and western Europe. Northern limit: southern zone 3.

229. **Artemisia furcata** Bieb. (*A. trifurcata* Steph.)

Fairly common on rocky alpine areas in the southwestern portion of the island. This species appears to differ from *A. glomerata* mainly in its elongated, spike-like inflorescences. Some specimens appear to be intermediates.

SPECIMENS EXAMINED: *Young 557*, Kongee; *643*, Boxer Bay. Also reportedly collected by Geist (Hultén 1950). Range: eastern Asia and western North America; very fragmented. Northern limit: not clear.

230. **Petasites frigidus** (L.) Franch.

Common to abundant on backshores, moist tundra, and lower alpine regions. While

the genus *Petasites* is notoriously difficult, all St. Lawrence specimens seem to fit well within *P. frigidus, sensu stricto.*

SPECIMENS EXAMINED: *Young 1, 721, 793,* Gambell; *21,* Tapphook; *162, 163,* Savoonga; *312, 313,* Northeast Cape; *397, 443,* Kialegak; *513,* Siknik. *Geist,* 1933, "western half." Several other reports. Range: not entirely clear because of taxonomic difficulties. Nearly circumpolar, absent from Greenland, may occur in eastern Canada (Cronquist 1946). Northern limit: northern zone 2.

231. **Arnica Lessingii** Greene

Fairly common on mesic tundra and lower alpine regions, rare elsewhere.

SPECIMENS EXAMINED: *Young 286,* Northeast Cape; *377,* Kialegak; *714,* Boxer Bay. Several other reports. Range: amphi-Beringean. Northern limit: not clear.

232. **Senecio congestus** (R. Br.) DC.

Occasional, usually found at the edges of brackish pools and lagoons, particularly on the south side of the island.

SPECIMENS EXAMINED: *Young 310,* Northeast Cape; *468,* Siknik. *Geist,* 1933, Boxer Bay. No other reports. Range: nearly circumpolar, absent in Greenland; arctic-alpine. Northern limit: zone 2.

233. **Senecio atropurpureus** (Ledeb.) Fedtsch.

Common on hummocks of wet tundra and in lower alpine areas; rare elsewhere. This taxon is extremely variable on St. Lawrence, but two rather distinct populations can be separated. One population has involucral bracts which are broad, rather short, and densely covered with short, pointed, multicellular purple hairs, with a trace of cobwebby white indument on the bracts. These specimens are always single stemmed and have no thick rootstock; the petals are usually long, broad, and clear yellow. The second population usually has longer, narrower involucral bracts; the stiff purple hairs are lacking, and the bracts are covered by a dense white indument, which may shade to somewhat shorter, thicker, pale brown hairs near the margin of the bracts. Specimens of this type commonly have several stems rising from a single rather thick rootstock. The petals are often, but not always, rather short and narrow; in the dried condition they are usually yellow-brown. The first population is apparently that which Hultén (1950, 1968a) treats as ssp. *atropurpureus,* while the second corresponds to ssp. *frigidus* (Richards.) Hult.

If one were to consider only the St. Lawrence material, there would be little justification in keeping both populations within the same species, as intermediates do not seem to occur on the island. However, in other parts of Alaska, and particularly in central Alaska and the Arctic Slope, intermediate specimens do occur. I believe that an intensive biosystematic study of this complex would indicate that at least two distinct species are involved. Possibly polyploidy or some similar phenomenon is responsible for some of the anomalous material from other parts of Alaska.

Within ssp. *atropurpureus* are two rather well-marked varieties. One, var. *tomentosus* (Kjell.) Cuf. (ssp. *tomentosus* (Kjell.) Hult., according to Hultén (1968a), is characterized by somewhat dentate leaves and a dense tomentum of brown hairs on the involucral bracts. This form was described from St. Lawrence Island material by Kjellman (1882), but it is apparently rare on the island, and I have not collected it there. It is common on the Alaskan mainland. Another variety, var. *dentatus,* has strongly dentate leaves. A single collection from St. Lawrence falls within this variety.

SPECIMENS EXAMINED: (ssp. *atropurpureus*): *Young* 59*x*, *96,* Tapphook; *307,* Northeast Cape; *536,* Siknik; *748,* Gambell. *Chamisso "Insula Sti. Laurentii." Coville & Kearney 1982,* Northeast Cape. *Geist,* 1933, Kangee. Several other reports. (Variety *tomentosus*): no specimens examined; several reports. (Variety *dentatus*): *Young 802,* Gambell; no other reports. (Subspecies *frigidus*): *Young 59, 85,* Tapphook; *197,* Savoonga; *275,* Fossil River; *366,* Kialegak; *474,* Gaedtuk; *611,* Boxer Bay. Several other reports. Range: Siberia and western North America; arctic-alpine. Northern limit: zone 2.

234. **Senecio resedifolius** Less.

Occasional on fell-fields and dry alpine areas. The corolla of the ray flowers varies considerably in length.

SPECIMENS EXAMINED: *Young 274*, Fossil River; 585, Gaedtuk; 686, Boxer Bay. *Geist*, 1933, Boxer Bay. Also reportedly collected by Chamisso (Hultén 1950). Range: Siberia and western North America, with a disjunct population in eastern Canada; arctic-alpine. Northern limit: northern zone 3, with some zone 2 stations.

235. **Senecio pseudo-arnica** Less.

Common to abundant on foreshores, less common on backshores. Most specimens are of short stature and bear a single head.

SPECIMENS EXAMINED: *Young* 83, Tapphook; *346*, Northeast Cape; *460*, Kialegak; *484*, Siknik; *650*, Boxer Bay; *731*, Gambell. Several other reports. Range: coastal areas of the Bering Sea and North Pacific. Disjunct populations in eastern Canada. Northern limit: not clear.

236. **Saussurea viscida** Hult.

Occasional on moist and dry tundra. Saint Lawrence Island is the type location for this species, which is characterized by viscid, not arachnoid, pubescence on the leaves (Hultén 1950). Most of the St. Lawrence specimens have this character, but it is not uncommon to find some arachnoid pubescence, particularly on the upper leaves of young shoots.

SPECIMENS EXAMINED: *Young 111*, Tapphook; *264*, Fossil River; 565, Gaedtuk; *1305*, Gambell. Several other reports. Range: Beringean region to western Mackenzie dist. Northern limit: not clear.

237. **Taraxacum ceratophorum** (Led.) DC.

The problems in the genus *Taraxacum* are so well known that they need not be commented on here. Haglund (*in* Hultén 1950) attributes 54 species of the genus to Alaska. More recently Hultén (1968a) claims that 11 major groups, most of which correspond to species, occur in Alaska. Five of these, *T. ceratophorum, T. lateritium, T. hyparcticum, T. alaskanum* and *T. kamtschaticum* are said to occur on St. Lawrence. I have seen none of the specimens on which these reports are based, but most of them are listed by Hultén (1950).

Among the specimens I have examined, there appear to be two reasonably constant types. Plants with narrow involucral bracts and fairly large appendages are here treated as *T. ceratophorum*, following Wiggins and Thomas (1962). This form is somewhat more robust than *T. alaskanum*, which is characterized by broader involucral bracts with the appendages small or lacking. *Taraxacum ceratophorum* is common on backshores and raised beaches and may be abundant on old village sites.

SPECIMENS EXAMINED: *Young 496*, Siknik; 669, Boxer Bay; *1450*, Gambell. Range: the genus *Taraxacum* is nearly ubiquitous. According to Hultén (1968a), *T. ceratophorum* is a circumpolar arctic-alpine form, reaching northern zone 2.

238. **Taraxacum alaskanum** Rydb. (*T. lyratum* (Led.) DC.)

Occasional on dry tundra and on the broader barrier beaches. None of the specimens examined have mature achenes, and the identification is based on the broad involucral bracts which have a much reduced appendage.

SPECIMENS EXAMINED: *Young* 98, Tapphook; 256, Savoonga. Range: probably eastern Asia and western North America. Northern limit: not clear.

SECTION II. FLORISTIC ZONATION IN THE ARCTIC REGIONS

Introduction

The most salient feature of the St. Lawrence Island flora is the comparative paucity of species included in it. The island's flora is now well-known, and the few species yet to be discovered must either be rare or of limited range. Most of them will probably be found on the south slopes of the mountains on the eastern end of the island. It seems reasonable to estimate that the total vascular flora of the island is in the neighborhood of 250 species. Many of these species are of rare or local occurrence on St. Lawrence. Hence, it is often possible to make an intensive collection over an area of several square miles and find no more than 125 to 150 species of plants. This is particularly true in the northwestern and northeastern portion of the island.

The flora of many mainland areas in Arctic Alaska and Siberia is much richer than that of St. Lawrence Island. At least 500 species of vascular plants are known to occur on the southwestern Seward Peninsula in an area comparable in size to St. Lawrence (Hultén 1968a), and about 75 species unknown on St. Lawrence occur in the vicinity of Cape Chaplino, Siberia, only about 40 sea miles away (Hultén, *loc. cit.*). Even in the few square miles of the Ogootoruk Creek drainage, which is 300 miles farther north than St. Lawrence, Johnson *et al.* (1966) collected over 300 species of vascular plants.

The point has been made elsewhere, but should be emphasized, that many of the species not known to occur on St. Lawrence are common and of considerable ecological importance on the nearby Alaskan mainland. Among the more notable examples are *Salix glauca, S. alaxensis, Spiraea Beauverdiana* and *Rhododendron camtschaticum.* The first three are abundant in mesic tundra and along watercourses throughout most of western Alaska. *Rhododendron camtschaticum* often forms nearly pure stands, sometimes several acres in extent, on the drier uplands of the Seward Peninsula.

Many of the species not known to occur on the island produce copious amounts of wind dispersed propagules (e.g., *Salix*), and there can be little doubt that they are regularly transported to St. Lawrence from the Siberian or Alaskan mainland. The absence of these species on the island must be attributed to currently acting ecological factors which inhibit their establishment. Support for this view is provided by the numerous species which are of rare and/or local occurrence on St. Lawrence, but which are important constituents of the vegetation of nearby mainland areas. This is particularly evident in the cases of such species as *Eriophorum vaginatum, Betula nana, Empetrum nigrum, Epilobium angustifolium, Ledum decumbens, Vaccinium uliginosum* and many others.

Since these species actually occur on St. Lawrence, but do not become

a significant part of the vegetation, there can be little doubt that the difference in their status on St. Lawrence, as compared to the adjacent mainland areas, is the result of differences in the environment of the areas involved. The large size and physiographic complexity of St. Lawrence Island indicates that a lack of suitable physical habitat is of little importance in limiting the ranges of the species mentioned above.

It is interesting to compare the flora of St. Lawrence Island with that of some other arctic areas. For example, there are over 200 species of vascular plants on the Pribilov Islands (Hultén 1968a), roughly the same number as on St. Lawrence, although the area involved is much smaller. The Pribilovs are situated in the Bering Sea, 300 miles south of St. Lawrence. Both areas have had a similar Pleistocene history in that both were included in the Bering Land Bridge, although the land connection to the Pribilovs may have been severed at a somewhat earlier date than that of St. Lawrence (Hopkins 1967). Many of the Beringean endemic species are found in both locations and their vegetation is similar. It is surprising, therefore, that the Pribilov flora contains over 20 genera and 75 species of vascular plants which are unknown on St. Lawrence. This means that of the more than 300 species included in the combined floras of St. Lawrence Island and the Pribilovs, less than 150 (or less than 50 per cent) are common to both areas. If the flora of St. Lawrence is compared to that of the south island of Novaya Zemlya, which also has a flora of 208 species (Tolmatchev 1936), about the same degree of similarity is found to exist. However, Novaya Zemlya is on the opposite side of the Arctic Ocean, has a history of recent intensive glaciation (Flint 1957), is several hundred miles farther north than St. Lawrence, and has little or no access to the richly endemic flora of the Beringean region. There are also several cases in which a circumpolar complex is represented in each area, but by closely related vicarious species. If these were merged, the floristic similarity between the two areas would be increased.

The similarity between the St. Lawrence Island flora and that of Wrangel Island is particularly striking. The flora of Wrangel Island, as presently known, includes 180 species (Hultén 1968a), of which the vast majority also occur on St. Lawrence. Many of the St. Lawrence species which are not known to occur on Wrangel Island are confined to a few isolated stations on the south side of St. Lawrence. Even if these rare or local species are considered, the St. Lawrence Island flora is much more similar to that of Wrangel Island than to that of the Pribilovs. Many more examples could be given to show that similarities and differences between various arctic floras are not strongly dependent on geographical proximity or the Pleistocene history of the areas under consideration. I interpret this to mean that the similarities and differences between the floras of these arctic areas are, to a considerable degree, the result of similarities and differences in the current environment of the areas, rather than historical and distributional factors. The evidence discussed below indicates that this generalization may be applicable to the

entire arctic flora. It then follows that at least a portion, perhaps the major part, of the arctic flora must be more or less at equilibrium with its environment. The species involved must have essentially filled their potential range under present conditions in the arctic.

The flora and vegetation of the arctic are relatively uniform and simple in comparison with other major geographical regions of the world. The tundra is the only vegetation formation and in the entire arctic there are hardly more than 1000 species of vascular plants known to occur (cf., Polunin 1959). A measure of the uniformity of the arctic flora is that over 600 of these species occur in arctic Alaska alone (Hultén 1968a). A considerable fraction of these species have a circumpolar range, and many species whose range is less than circumpolar are nevertheless widespread.

It is important to note that practically no species are endemic to the higher arctic regions. Along a transect from the southern edge of the arctic to the shores of the polar sea, certain species drop out of the flora as one travels northward. However, species which drop out are seldom replaced by new ones, as would be expected in temperate or tropical regions. Instead, the more northerly part of the transect becomes increasingly depauperate. On certain large islands in the Arctic Ocean there are less than 50 species, and there is little or no continuous vegetation. This suggests that competition may be a factor of little or no importance in the disappearance of certain species from the upper portions of the arctic. If the disappearance is ecologically induced, as seems to be the case, the limiting factors which operate must be non-biotic—for example, climate.

It is suggested that the northward spread of species of arctic plants is controlled by the interaction of a very few environmental factors, perhaps even a single factor. An expected result is that groups of species, not necessarily of close taxonomic relationship but with similar northern limits of distribution, may be found. In this study, I have proceeded on the assumption that if a reasonable proportion of arctic plant species, particularly those with extensive ranges, could be placed in coherent groups with similar northern geographic limits, such groupings could be used to define zones of varying degrees of depauperateness in the arctic flora. Once established, these zones would be predictive to the extent that the presence or absence of a relatively few common species would designate to which zone an area belongs. It would also be possible to predict, with some degree of accuracy, what other species would be expected to be found in the area, and, more importantly, what species would not be expected to occur there. If it is correct to assume that the northern limits of species distributions are strongly influenced by a relatively simple set of limiting factors, it is to be expected that the patterns formed by groups of species with similar northern ranges are correlated with some ecological factor or group of factors, such as a climatic parameter. A great amount of distributional data for the arctic species of vascular plants have recently been summarized in the form of

dot maps by such workers as Hultén (1958, 1962), Tolmatchev (1960–1966) and Porsild (1964). With these maps, it is possible to examine in detail, the ranges of a large number of species, and to see the similarities and differences. Ultimately, significant patterns of distribution are discernible.

In the following section, major patterns of distribution that occur in the arctic flora are discussed. It is evident that the arctic does, in fact, have distinct zones of increasing depauperateness of vascular plant species from south to north. Evidence is presented which indicates that the progressive loss of species from south to north is closely related to the amount of warmth available during the summer growing season.

Concentricity of Northern Limit of Distribution of Many Arctic Plant Species

An examination of the published distribution maps will show that few of the circumpolar or widespread species of arctic plants are uniformly distributed throughout the entire arctic. Instead, it is the rule, rather than the exception, that a species will have one or more gaps in its distribution in the more northern parts of the arctic. Also, it is evident that the locations of these gaps are often nearly identical for a number of species which are taxonomically unrelated. For example, *Equisetum variegatum*, *Eriophorum angustifolium*, *Dryas integrifolia* and *Cassiope tetragona* (Fig. 4, 5, 6, 7) are all of nearly universal distribution throughout the North American arctic. All are usually among the most common species at any given station. However, none of these species is known to occur in one small area in the northwestern corner of the Canadian Arctic Archipelago. This area includes Elif Ringnes and Amund Ringnes Islands and the smaller Brock, Borden, Mackenzie, King, Lougheed, and Meighen Islands, as well as parts of Prince Patrick, Melville, Bathurst, Devon, and Axel Heiburg Islands. There are a number of other species whose ranges in northern Canada are practically identical to those of the four examples given.

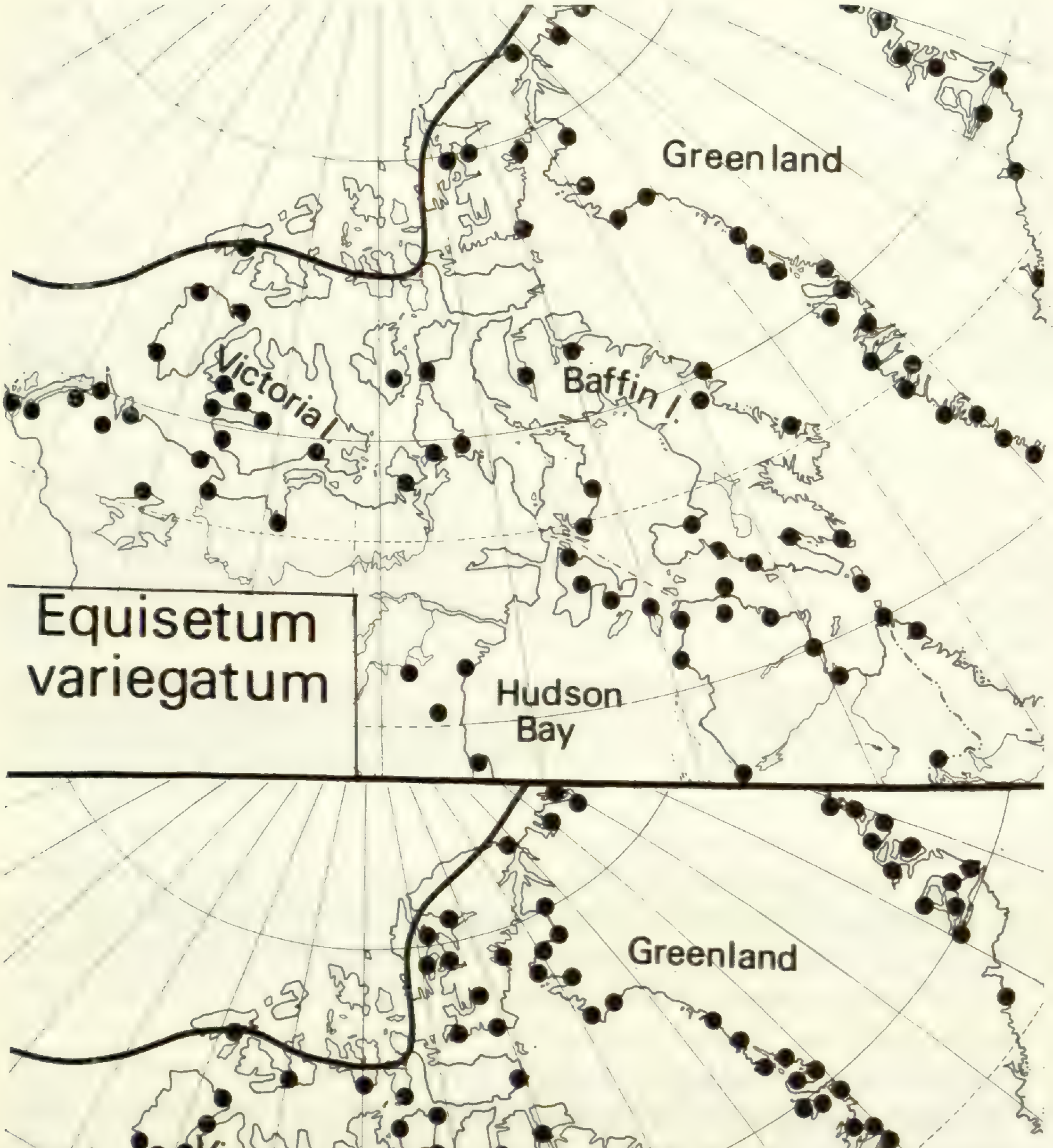
A further examination of the distribution maps indicates that, among species which are widespread in arctic North America, there is an entire series of groups of plants whose northern range limits are similar. These groups are easily placed in a natural sequence where the gaps in their distribution increase in size until the last groups are made up of species which are not known to occur in the Canadian Arctic Archipelago. A general picture of this can be seen in Fig. 8, where the northern limits of distribution of a number of widely distributed North American arctic species are plotted.

The evidence supports the conclusion that many species, which are common and widespread throughout much of the North American arctic, drop out of the flora of a north to south transect in a definite sequence. The sequence is approximately the same whether the transect is drawn in Alaska, the Canadian Arctic, or Greenland. However, the point at which a particular species drops out is not correlated with any particular latitude.

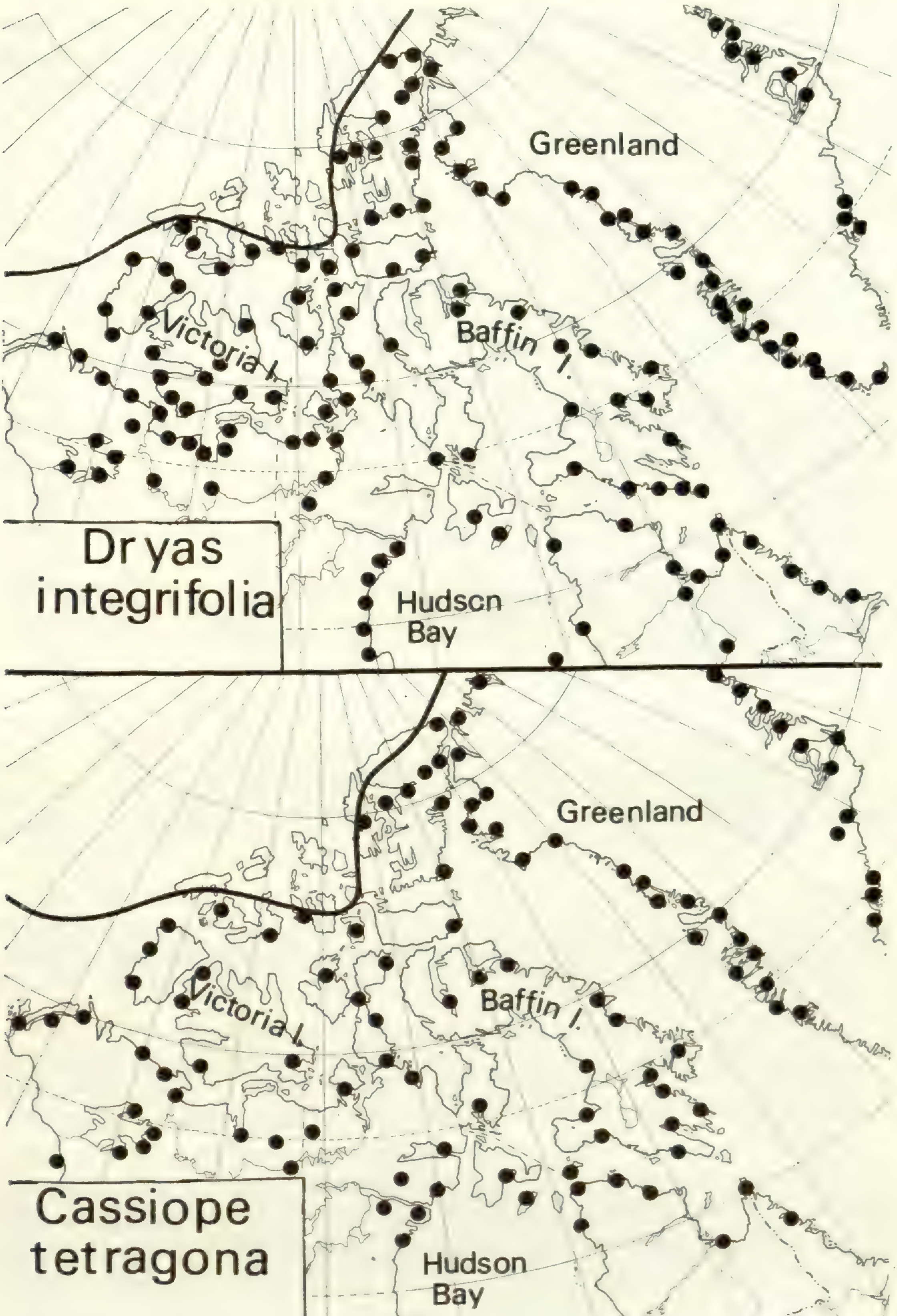
The distance over which parts of the sequence are completed is also subject to much variation. For example, in Alaska, the northernmost station for *Rhododendron lapponicum,* is only 50 miles north of the northernmost station for *Epilobium angustifolium,* but in West Greenland the range of *R. lapponicum* extends about 500 miles north of that of *E. angustifolium.*

In this study, the logical next step was to determine whether the same situation as that described above would hold true on a circumpolar basis. Comparing distributions over the entire arctic is difficult for several reasons. The number of species which can be compared is considerably reduced, as it is necessary to use only common circumpolar species to make a valid worldwide comparison. In addition, no detailed data have been published on the Asiatic distributions of a number of circumpolar species. For this reason, monocotyledons may seem to be over-represented in the following discussion, simply because there are more accurate distributional data available for them than for dicotyledons. Also, there may be a great deal of variation in a given species when it is treated over its entire circumpolar range. This presents taxonomic difficulties when discussing the range of a given species. Allied to this is the problem of regional differences in the taxonomic treatment of the species involved. Finally, geographical differences between the Eurasian and North American continents add a complicating factor. In North America, the arctic regions form a compact unit including Greenland and most of northern Canada, with extensions along the coast of Labrador and northern and western Alaska. On the Eurasian continent, however, the arctic region consists of a narrow and somewhat discontinuous strip along the arctic coast of the mainland, and then several more or less isolated islands and archipelagoes within the Arctic Ocean. The ranges of the tundra species are therefore often rather disrupted in Eurasia, particularly along the northern coast of Siberia. The sequential loss of a group of species may take place over a south to north distance of 1000 miles or more in Greenland or Canada, whereas the same species loss may take place over such a short distance (often less than 100 miles) in arctic Siberia that the sequence is either disrupted or not visible on a large scale map. Even with the handicaps noted above, when the total ranges of the common circumpolar species are plotted (see Fig. 9–16), it can be seen that the same general situation described for North America holds true throughout the entire arctic.

As might be expected, because of the geographical differences indicated above, depauperization of the arctic flora from south to north is not particularly evident on the Eurasian mainland. It is usually not until the arctic islands are considered that a significant reduction in the number of plant species is evident. Thereafter, loss of species takes place rapidly. Some of the Soviet archipelagoes support the most depauperate flora in the entire arctic. Only 36 species of vascular plants have been reported from Franz Josef Land (Hannsen & Lid 1932), and apparently the Severnaya Zemlya archipelago, in spite of its comparatively large geo-



FIGS. 4 AND 5. Range of *Equisetum variegatum* and *Carex misandra* in arctic Canada and Greenland.



FIGS. 6 AND 7. Ranges of *Dryas integrifolia* and *Cassiope tetragona* in arctic Canada and Greenland.

graphical area, supports even fewer species. This is not the result of geographical isolation, as is indicated by the fact that the much smaller and more isolated Svalbard archipelago, at about the same latitude, has a vascular flora of over 150 species (Rönning *in* Löve & Löve 1963).

A final point on the progressive loss of species from south to north is that the phenomenon is not confined to the circumpolar species. Most arctic species of vascular plants whose ranges are less than circumpolar have northern range limits which essentially parallel those of the circumpolar species. Therefore, a group of several species of less than circumpolar range may have an aggregate range whose northern limit is comparable to that of a single circumpolar species. Wide ranging species whose ranges are less than circumpolar can usually be assigned to groups in essentially the same manner as can circumpolar species, with respect to the northern limit of their range.

FIG. 8. Northern limits of distribution (reading from south to north) of: *Eleocharis acicularis, Pedicularis lapponica, Tofieldia pusilla, Pyrola grandiflora, Melandrium affine,* and *Juncus biglumis*

DIVIDING THE ARCTIC INTO FLORISTIC ZONES

The concept of the division of the northern parts of the world into floristic zones is not new. Geographers define the arctic as being the treeless tundra areas in the far north. The timberline, or the poleward limit of arborescent conifers, forms a boundary between the arctic and subarctic zones. As the timberline is essentially the northern limit of range of the family *Pinaceae,* specifically the genera *Picea* and *Larix,* it constitutes a definite floristic boundary, although it is thought of as a vegetational boundary. The boundaries proposed here are a continuation of the same line of reasoning that considers the timberline the arctic-subarctic boundary. The essential difference is that within the arctic region there is no vegetational boundary comparable to the timberline. Zone boundaries within the arctic must be drawn almost entirely on a floristic basis, and the choice of species used to define the boundaries is somewhat arbitrary. The positions of the zone boundaries could be moved north or south,

depending on the species or groups of species used, and a number of zone boundaries could be drawn. No matter how many are used, or what species groups define them, the boundaries should theoretically retain the same relationship to each other because of the concentricity of the northern limits of the ranges of the species involved.

The system of four zones proposed here (Fig. 17) seems to be a reasonable compromise in the light of the available evidence. If more zones are drawn, there is an implication that the zonation system is more accurate than the distributions of the plants, as they are presently known, would warrant. Also, a considerable number of species begin to show up whose northern range limits are anomalous because they cross zone boundaries. It is true that fairly large numbers of species have northern range limits which characteristically fall within a particular portion of one of the proposed zones, and one might be tempted to increase the number of zones or draw subzones because of this. However, it seems more reasonable to mention that the northern limit of range of some species is, for example, in southern zone 2, or northern zone 4, with no implication that a well-delineated subzone exists. If less than four zones are drawn, the differentiation between the lower and upper portions becomes too great, and the zones become too inclusive.

There is some justification for treating the taiga region as a fifth zone. However, in the subarctic, the ranges of most species of plants are much more fragmented than in the higher latitudes. Only a small fraction of the species involved have ranges which form patterns comparable to those used to define the arctic floristic zones. The timberline would make a reasonable northern boundary for a fifth zone, but the southern boundary would be difficult to define on a worldwide basis. The proposed system of floristic zonation based on concentricity of the northern limits of distribution can be effectively applied only in the polar regions. The explanation for this seems to be that the northern limit of distribution of most polar plants is largely dependent on a single limiting factor, the amount of available warmth during the growing season. This is discussed in detail later.

In temperate regions, coastal and high altitude areas often support a flora which includes many boreal and even arctic elements. Similarly, boreal elements occur in the arctic, particularly in coastal regions. Small islands and sea coasts often support a flora characteristic of a zone farther to the north than adjacent mainland areas. Most of these areas are too small to be taken into account here, but it should be noted that the zone of an area should not be based only on collections from coastal areas.

Description of the Zones. The boundaries of the four zones are given in Fig. 17. In terms of land area, zone 1 is the smallest of the four. It includes a few island groups and scattered islands in the Arctic Ocean; the most important areas are Franz Josef Land, Severnaya Zemlya and the northern edge of the Taimyr Peninsula near Cape Chelushkin, most of the New Siberian Islands and some of the islands in the northwest corner of

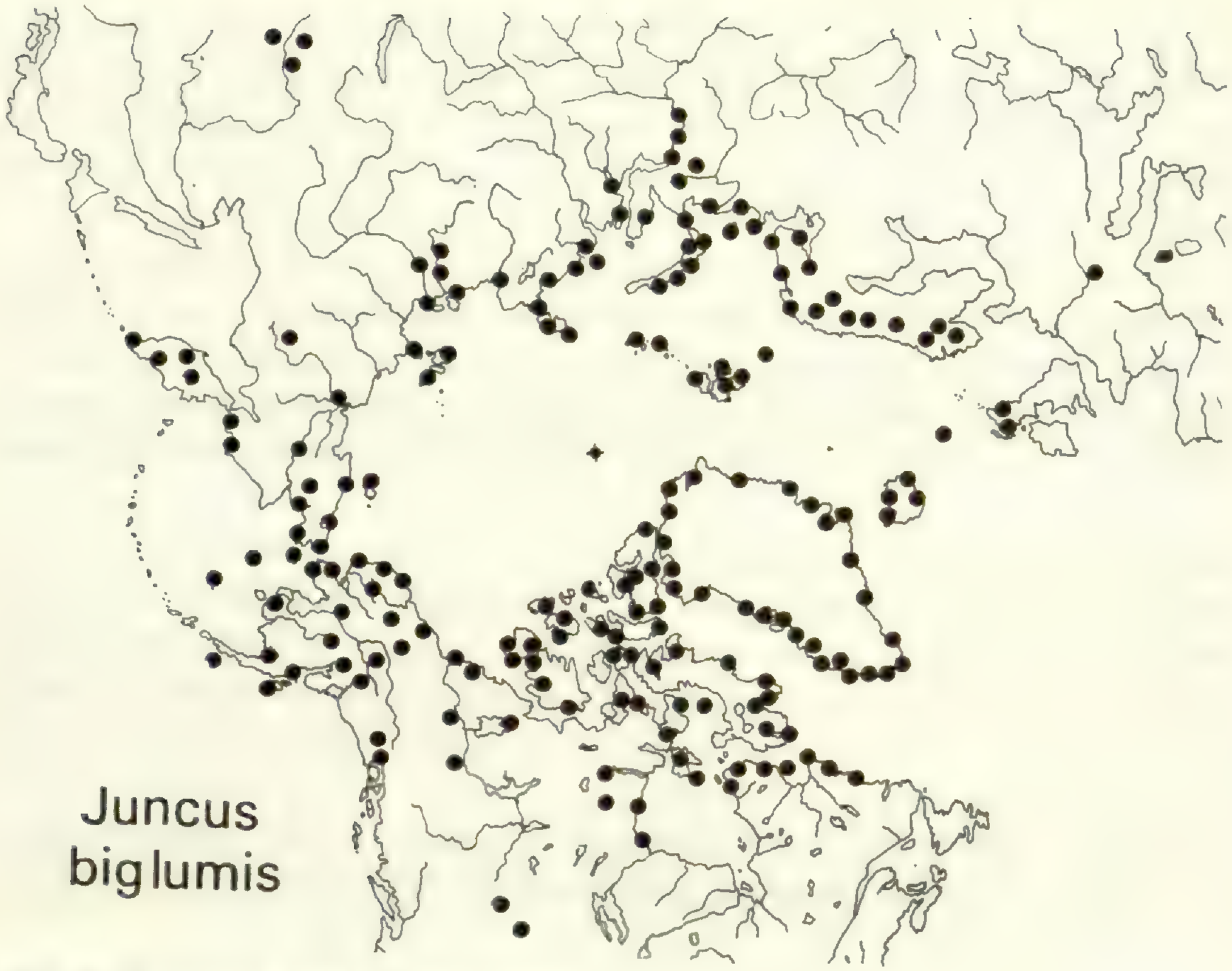


FIG. 9. Circumpolar range of *Juncus biglumis*.

FIG. 10. Circumpolar range of *Oxyria digyna*.

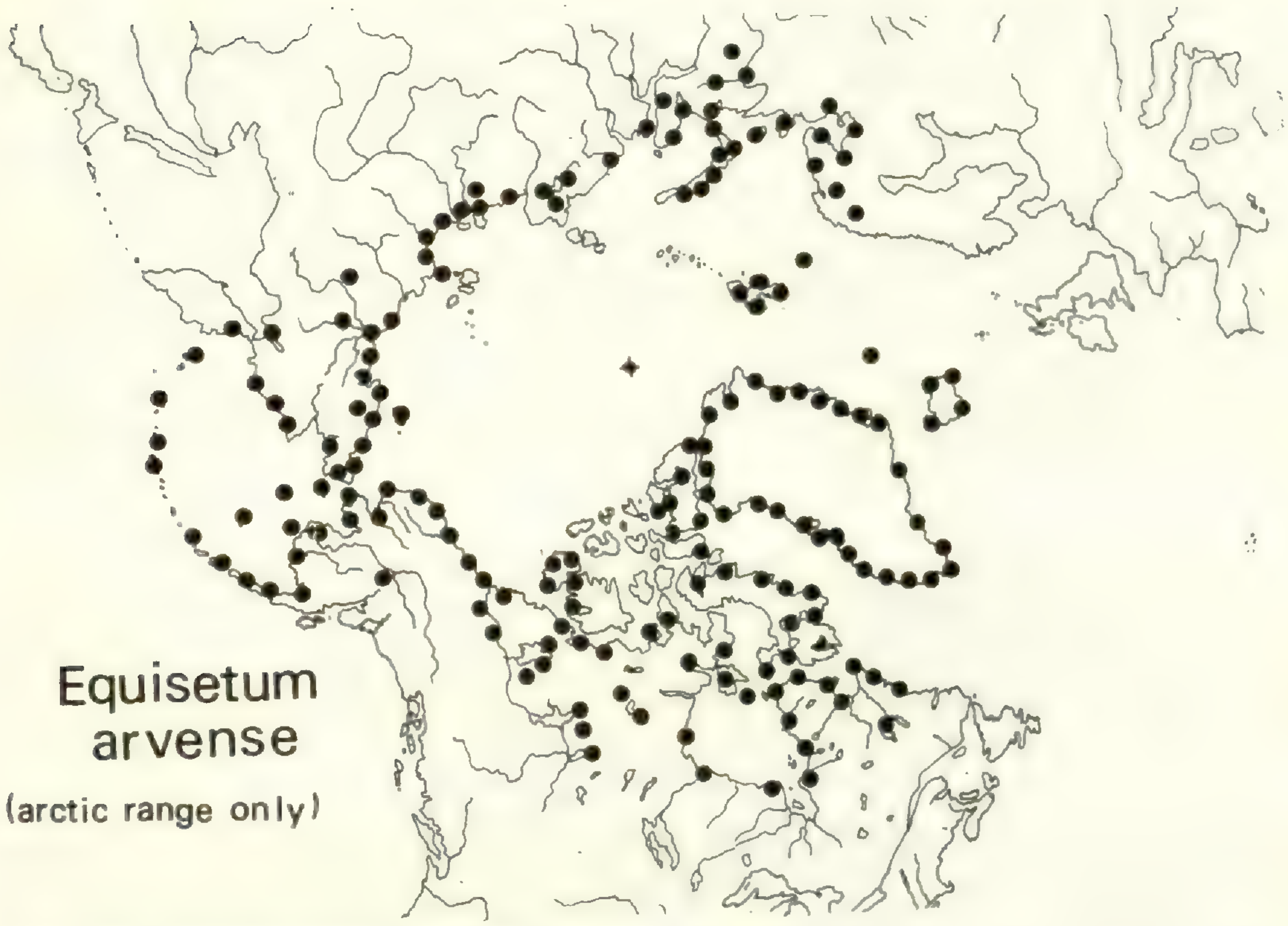


FIG. 11. Circumpolar arctic range of *Equisetum arvense*. Note lack of stations of this species in northwestern Canada, Franz Josef Land, Severnaya Zemlya and northern New Siberian Islands.

FIG. 12. Circumpolar range of *Carex misandra*. The northern limit of this species is similar to that of *Equisetum arvense*.

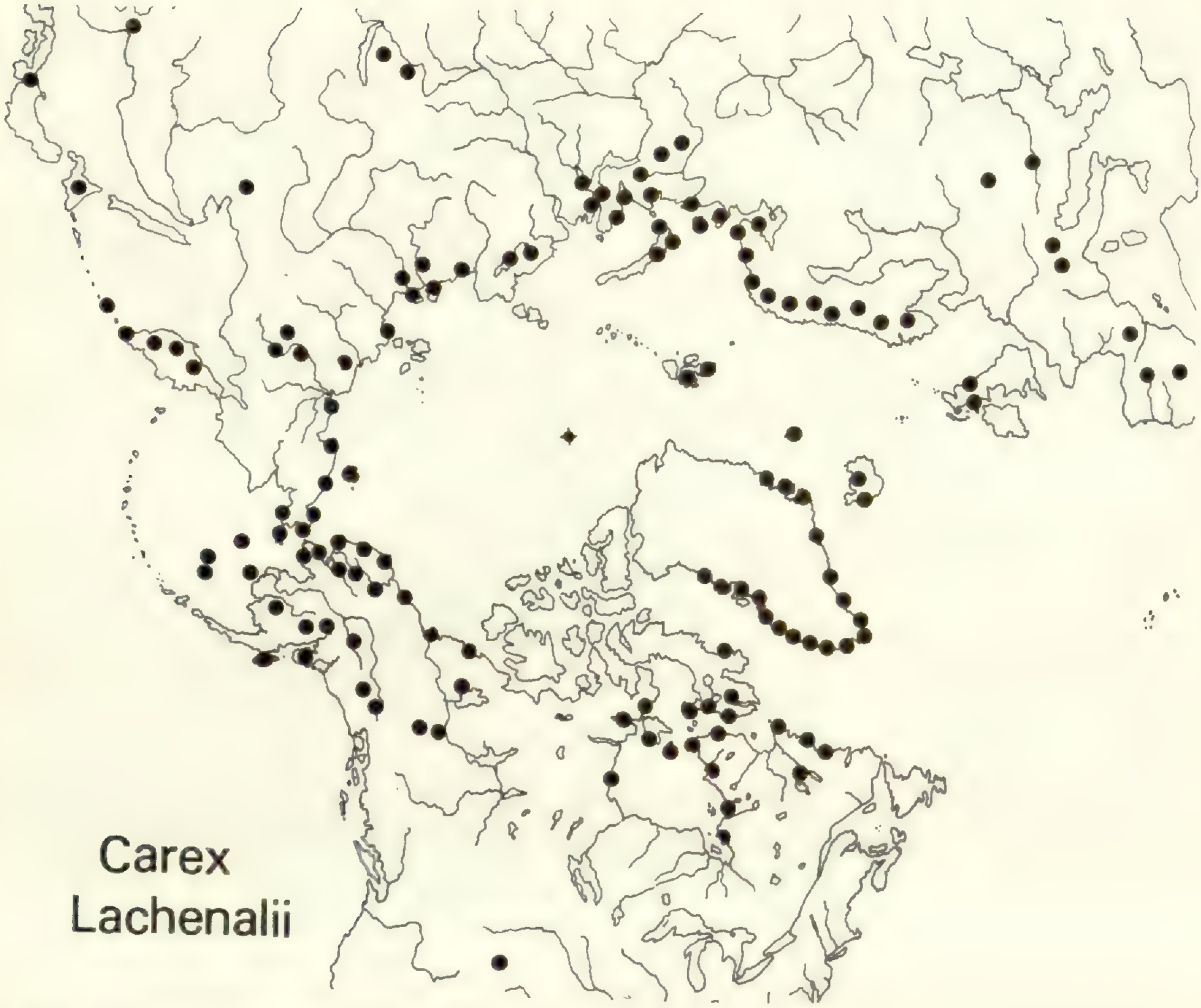


FIG. 13. Circumpolar range of *Carex Lachenalii*.

FIG. 14. Circumpolar range of *Pyrola grandiflora*.

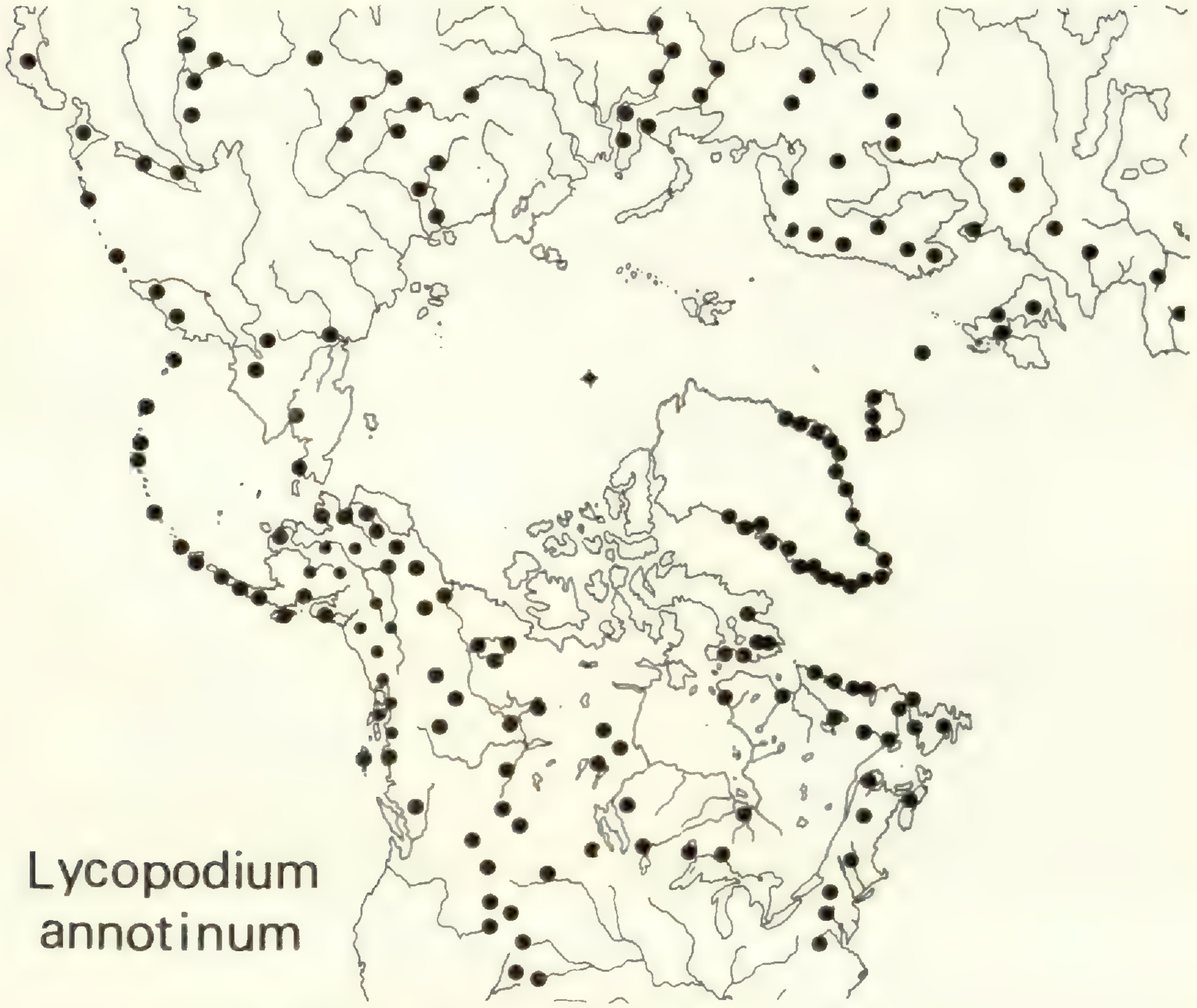


FIG. 15. Circumpolar range of *Lycopodium alpinum*.

FIG. 16. Circumpolar range of *Calamagrostis lapponica*.

the Canadian Arctic. Areas on the coastal fringe of northernmost Greenland and Ellesmere Island could be placed in zone 1, as well as some of the small islands in the northeastern part of the Spitzbergen Archipelago.

The floras of all zone 1 areas are exceedingly impoverished, normally including no more than 50 species of vascular plants. About 50 species are known to occur on Elif Ringnes Island, while other nearby islands have fewer species (Saville 1961). Thirty-six species have been collected in the entire Franz Josef archipelago (Hannsen & Lid 1932). Although exact figures are not available, the flora of Severnaya Zemlya seems to be even more impoverished. No vascular cryptograms are known to occur in zone

TABLE 1. COMMON CIRCUMPOLAR SPECIES WHOSE NORTHERN LIMIT IS USUALLY IN ZONE 1.

Alopecurus alpinus	Minuartia rubella
Phippsia algida	Ranunculus sulphureus
Deschampsia caespitosa *sensu lato*	Papaver radicatum *sensu lato*
Arctagrostis latifolia	Cardamine bellidifolia
Poa arctica *sensu lato*	Draba alpina
Poa alpigena	Draba macrocarpa
Dupontia Fischeri *sensu lato*	Draba subcapitata
Carex ursina	Saxifraga caespitosa
Juncus biglumis	Saxifraga hirculus
Luzula arctica	Saxifraga cernua
Luzula confusa	Saxifraga flagellaris
Salix arctica *sensu lato*	Saxifraga nivalis
Oxyria digyna	Saxifraga rivularis
Stellaria Edwardsii	Saxifraga oppositifolia
Cerastium aff. arcticum	Potentilla hyparctica *sensu lato*

1 areas, although several species reach the northern edge of zone 2, and the northern limits of the ranges of *Equisetum arvense* and *E. variegatum* coincide almost perfectly with the boundary between zone 1 and zone 2. Most of the species found in zone 1 have a circumpolar, or nearly circumpolar, range. They tend to be species of common occurrence in a wide variety of habitats throughout the arctic regions. Few of the species which occur in zone 1 form extensive colonies, and closed stands of any sort are rare or absent. A list of species commonly found in zone 1 is given in Table 1.

Zone 2 includes the northernmost land areas in the world, northern Greenland and Ellesmere Island. Nevertheless, most zone 2 areas support a much richer flora than does zone 1. The flora of a typical zone 2 area usually includes 75 to 125 species of vascular plants. The area also includes most of the northern part of the Canadian Arctic Archipelago, Greenland north of about 79° lat. on the west coast and 76° on the east, most of the Spitzbergen Archipelago, northern Novaya Zemlya, the northern portions of the Yamal and Taimayr Peninsulas, and the southern islands in the New Siberian Islands. A small area in the vicinity of Point Barrow, Alaska, supports typical zone 2 flora. Wrangel Island seems best placed in zone 2; its flora is much richer than that of other zone 2 areas, but this is mainly

attributable to the great variety of habitats on the island and its close proximity to the floristically rich Beringean region. Most of the characteristic zone 3 species are not known to occur on Wrangel Island.

TABLE 2. COMMON CIRCUMPOLAR SPECIES WHOSE NORTHERN LIMIT IS USUALLY IN ZONE 2.

Cystopteris fragilis	Melandrium affine
Equisetum arvense	Ranunculus hyperboreus
Equisetum variegatum	Ranunculus pedatifidus
Lycopodium selago	Ranunculus nivalis
Hierochloe alpina	Ranunculus pygmaeus
Hierochloe pauciflora	Cochlearia officinalis
Trisetum spicatum *sensu lato*	Eutrema Edwardsii
Puccinellia phryganodes	Cardamine pratensis
Eriophorum angustifolium *sensu lato*	Braya purpurascens
Eriophorum Scheuchzeri	Draba lactea
Kobresia myosuroides	Saxifraga foliolosa
Carex rupestris	Saxifraga hieracifolia
Carex aquatilis	Astragalus alpinus
Carex misandra	Epilobium latifolium
Carex saxatilis	Cassiope tetragona
Polygonum viviparum	Pedicularis capitata
Sagina intermedia	Armeria maritima
Stellaria humifusa	Senecio congestis
Melandrium apetalum	Taraxacum ssp.

Zone 2 includes most of the area traditionally called the high arctic. The flora here consists mainly of circumpolar or wide-ranging species, so that there is a strong similarity between the floras of various zone 2 areas. In contrast to zone 1, at least seven species of vascular cryptograms are known to occur in zone 2. A list of species characteristically found in zone 2 but whose ranges do not reach zone 1 is given in Table 2.

Zone 3 includes an area which is transitional between the floristically depauperate high arctic regions of zones 1 and 2 and the rich low arctic zone 4. Zone 3 floras, from all but the most remote areas, include well over 100 species. Even the isolated floras from the Inner Fjord District of Spitzbergen and the Eureka area of Ellesmere Island, both at nearly 80° north, each include approximately 150 species. Less isolated zone 3 areas may support a flora of 250 or more species. Included in zone 3 are most of the southern and eastern portions of the Canadian Arctic Archipelago, as well as some mainland areas such as Melville and Boothia Peninsulas. Also included is West Greenland north of Disco Bay, East Greenland north of Scoresby Sound, the southwestern portion of Spitzbergen, Bear Island, Jan Mayan Land, southern Novaya Zemlya and Vaigatch Island, and a narrow, and somewhat discontinuous strip stretching from the Yamal Peninusla across arctic Siberia to the Bering Strait and along the north coast of Alaska. This coastal strip is usually less than 50 miles wide, and it is interrupted by zone 4 areas at the mouths of the larger rivers, such as the Lena, Olenek and Colville.

TABLE 3. COMMON CIRCUMPOLAR SPECIES WHOSE NORTHERN LIMIT IS USUALLY IN ZONE 3.

Woodsia alpina
Woodsia glabella
Dryopteris fragrans
Equisetum scirpoides
Calamagrostis neglecta
Calamagrostis purpurascens
Poa alpina
Poa glauca
Festuca rubra
Elymus arenarius *sensu lato*
Eriophorum callitrix
Eriophorum brachyantherum
Eriophorum russeolum
Eriophorum vaginatum
Kobresia simpliciuscula
Carex scirpoidea
Carex Lachenalii
Carex glareosa
Carex subspathacea
Carex rariflora
Carex capillaris
Carex Bigelowii
Juncus triglumis
Juncus castaneus
Luzula Wahlenbergii
Tofieldia pusilla
Tofieldia coccinea
Salix reticulata
Salix glauca
Salix lanata
Betula nana *sensu lato*
Koenigia islandica
Montia fontana
Honckenya peploides
Draba hirta
Ranunculus aquatilis *sensu lato*
Ranunculus lapponicus
Draba cinerea
Epilobium davuricum
Hippurus vulgaris
Empetrum nigrum
Pyrola grandiflora
Ledum decumbens
Loisleuria procumbens
Arctostaphylos alpina
Vaccinium vitis-idaea
Diapensia lapponica
Pedicularis lapponica
Artemisia borealis
Arnica alpina

In zone 3, differentiation between the floras of the various sectors of the arctic is much more marked than in zones 1 and 2. This is partially accounted for by the fact that there are no zone 1 and only small zone 2 areas between the western Canadian Arctic and the New Siberian Islands. Thus, with the exception of Wrangel Island, the highest zone reached by the richly endemic Beringean flora is zone 3. The presence of Beringean endemics on Wrangel indicates that many of these species have become adapted to live in the conditions of zone 2 areas. A list of species characteristically found in zone 3 but which do not normally reach zone 2 is given in Table 3.

Zone 4 includes most of the area traditionally considered to be the low arctic. In contrast to the other zones, it is primarily restricted to mainland areas. Its land area is much larger than any of the others, being approximately equal to their total. The composition of zone 4 floras varies greatly from one sector to another, tending to obscure the concentricity of the northern limits of the ranges of zone 4 species. The problems which make the theory of zonation inapplicable to the temperate regions becomes evident in zone 4. Although its flora contains several times as many species as zones 1 and 2, the percentage of circumpolar species drops off sharply and the number of characteristic species is hardly greater than for the other zones. Otherwise, it might be possible to separate it into two zones, since the difference in flora and vegetation between the upper and lower

edges is often quite striking. There is also a noticeable difference between the floras of zone 4 areas in continental climatic conditions and floras

TABLE 4. COMMON CIRCUMPOLAR SPECIES WHOSE NORTHERN LIMIT IS USUALLY IN ZONE 4

Gymnocarpium dryopteris	Carex atrata
Botrychium lunaria	Carex vaginata
Lycopodium alpinum	Juncus filiformis
Lycopodium annotinum	Juncus alpinus
Lycopodium clavatum	Luzula parviflora
Lycopodium complanatum	Alnus ssp.
Selaginella selaginoides	Betula glandulosa *sensu lato*
Equisetum fluviatile	Stellaria calycantha *sensu lato*
Equisetum palustre	Sagina nodosa
Equisetum sylvaticum	Coptis trifolia
Juniperus communis	Ranunculus reptans *sensu lato*
Potamogeton filiformis	Rorripa islandica
Potamogeton gramineus	Rubus arcticus
Potamogeton perfoliatus	Potentilla Egedii
Hierochloe odorata	Sibbaldia procumbens
Agrostis borealis	Viola epipsila *sensu lato*
Calamagrostis canadensis	Epilobium angustifolium
Calamagrostis lapponica	Epilobium palustre
Eleocharis acicularis	Myriophyllum exalbescens
Scirpus cespitosus	Pyrola secunda
Carex bicolor	Pyrola minor
Carex brunnescens	Andromeda polifolia
Carex capitata	Menyanthes trifoliata
Carex dioica	Veronica alpina
Carex chordorrhiza	Pedicularis labradorica
Carex rotundata	Linnaea borealis

from maritime situations. However, the circumpolar element is essentially similar.

Zone 4 floras typically include over 200 species of vascular plants. Some of the richer floras, such as those of the southern Seward Peninsula, may contain over 500 species, about twice as many as are found in the richest zone 3 floras. Zone 4 includes nearly all of the mainland of arctic Canada, but only a few small areas in the southernmost part of the Canadian Arctic Archipelago. Also included are Greenland south of about 70° north, most of Iceland, the coast of northernmost Scandanavia and the Murman Coast, and a narrow strip along the northern edge of the Eurasian continent from the Kanin Peninsula to the Chukchi Peninsula, then south along the Bering Sea coast of eastern Siberia. In addition, the Bering and Chukchi seacoast of Alaska and central Alaska from the Brooks Range northward are included. The Aleutian Islands, Komandorsky Islands, part of coastal Kamtchatka, and some areas along the coast of the Sea of Okhotsk are also included in zone 4. A list of some of the more characteristic circumpolar or widespread zone 4 species is given in Table 4.

Because species can be placed accurately in appropriate zone categories on the basis of their northern limits of distribution, only a fraction of the

FIG. 17. Boundaries of the four proposed arctic floristic zones. Zones 2 and 4 are shaded. Zones 1 and 3 are unshaded.

total flora of an area need be known to ascertain to which zone the area belongs. For example, Johansen (1924) in a discussion of the vegetation of Herschel Island mentions a number of species which he says are of common occurrence there. However, the list is not a complete tabulation of the flora. The majority of the species listed are those typical of the arctic and commonly occurring in the higher zones. Also mentioned, however, are several species such as "*Lupinus nootkatensis*" (*L. arcticus*), "*Phaca frigida*" (*Astragalus americanus*), *Bupleurum americanum* and *Achillea borealis*, all of which occur in zone 4 in northwestern North America. If the flora of Herschel Island is compared with that of Barter Island, which lies about 100 miles westward along the coast of Alaska, it will be found (Wiggins & Thomas 1962) that none of the species mentioned above is known to occur on Barter Island, or are any other zone 4 species found there. One can therefore conclude that Barter Island is in zone 3 (or possibly a higher zone) and that the boundary between zone 4 and zone 3 intersects the arctic coast somewhere between the two islands.

Correlation of Floristic Zones with Ecological Factors

The lack of correlation of the floristic zones with strictly historical or geographical factors has already been mentioned. There can be no doubt that ecological factors are of major importance in controlling the northward expansion of the ranges of arctic plants. However, the factors which have determined the present range of non-circumpolar species obviously must contain historical components as well.

It has been noted that the arctic timberline forms the southern boundary of zone 4 and it is essentially a floristic boundary in that it is the northern limit of the genera *Picea* and *Larix*. One might expect that other floristic boundaries in the arctic would be correlated with ecological factors in much the same way. But research (cf., Kimball & Good 1955; Hustich 1953; Hopkins 1959b) indicates that the major ecological factor involved is the amount of available summer warmth. This was first proposed by Koeppen (1936, the latest statement of a much older theory) and Merriam (1894). Koeppen noted that there is a strong correlation between the location of the arctic timberline and the 10° C isotherm for the warmest month of the year. How exact this correlation is can be judged from the map (Fig. 18). The location of the timberline is shown quite accurately but that of the 10° C July isotherm is much more difficult to plot and over fairly long distances it is drawn between stations by inference. Local microclimatic or special conditions caused by altitude cannot be taken into account but it can be assumed that, within these limitations, the location of the 10° C July isotherm is reasonably accurate, perhaps to within two degrees C.

In the far north the timberline lies south of the 10° C July isotherm. The greatest distance occurs in areas near large bodies of water and is apparently an effect of maritime climatic conditions. Various systems have been proposed to describe a climatic boundary which approximates the timberline more closely than does the 10° C July isotherm. The best known of these is the Nordenskjold line (Nordenskjold & Meckling 1928), which takes winter as well as summer temperatures into account. Merriam (1894) proposed that the northern limits of the ranges of many species are more dependent on the total amount of warmth available during the growing season than on any temperature level at a specific time. Hopkins (1959a) used a similar approach by showing that the timberline in western Alaska can be closely correlated with the number of degree days above 10° C during the summer. The July isotherm for a given temperature does not adequately express the amount of available warmth. In some maritime areas, August is the warmest month of the year, and there is a good deal of variation in temperatures for other months of the growing season between areas whose July mean temperature is comparable. A better means of expressing the amount of warmth must be developed to correlate the northern limit of the ranges of plants and the amount of available warmth during the growing season.

FIG. 18. Approximate location of the 10° C isotherm for the month of July (black line) and arctic tundra areas (shaded). Data from several sources.

It also must be recognized that standard data from weather stations are not an entirely adequate index of the temperature regime of a given area. Temperature data at weather stations are normally gathered at a height above the ground of several feet, while the effective temperature for tundra plants is the temperature near the soil surface. Standard weather station data must be used because nothing else is available, although they are not particularly accurate for the purpose.

One method of determining warmth during the growing season is to sum the mean temperatures of all the months having a mean temperature above 0° C. This gives a more accurate figure than that of the isotherm, it can be computed rapidly from published data, and does not imply an unjustified degree of accuracy. For convenience, the aggregate of mean temperatures above 0° C (in degrees C) will be referred to as *a*. The use of 0° C for a base point from which to compute *a* is arbitrary. Since permanent ice and snow normally cover areas in which the mean temperature does not rise above 0° C for any month of the year, a value of

a=0 corresponds closely with the absolute limit of vegetation. However, there is no implication that 0° C is a critical limit for plant growth. In any case, the summer temperature curves of arctic stations are regular enough so that a computed from a base point of 0° C is well-correlated with a similar figure computed from a base point within a few degrees of 0° C (see Fig. 19–23).

These figures show climatographs from a series of arctic stations at about timberline and in each of the four floristic zones. The location of each station is given in Fig. 24. Several conclusions can be drawn from the data presented. First, there is no significant correlation between annual mean temperature and the floristic zones. Mean annual temperatures in some zone 1 areas are actually higher than in some timbered and timberline areas (see Table 5). This suggests that winter temperatures are not a significant factor related to floristic zonation. Second, mean annual precipitation shows no significant correlation with the floristic zones, although there is some tendency for precipitation to be less in the higher arctic regions. Third, summer temperatures are strongly correlated with the zones. It is not possible to assign given values for the mean temperature for any month of the year to given zones, but it is strongly suggested that the summer temperature regime of each of the zones falls within rather exact limits of a. Zone 1 stations characteristically have an a between 0 and 6, zone 2 between 6 and 12, zone 3 between 12 and 20, zone 4 between 20 and 35, and stations in timbered country usually have an a of over 35. Values of a for some additional stations are given in Table 5.

Unexpectedly low a values occasionally occur, as in the case of Resolution Island, with an a of 11, although adjacent parts of Baffin Island are in zone 4 and the lower part of zone 3. Cases of this sort are almost always related to an extremely maritime climate. As noted, the floras of these areas are impoverished, and the areas can be thought of as "islands" of a higher zone. The situation is reversed in a few areas with a highly continental climate. This explains why parts of Ellesmere Island, at about 80° north, are in zone 3. Peary Land, Greenland, the northernmost land in the world, has a highly continental climate. Although it lies at about 83° north, both the flora and a value have some characteristics of a zone 3 area.

There is no significant correlation between the floristic zones and day length. If day length were an important factor in controlling the distribution of arctic plants, it would tend to even out some of the major northward and southward extensions of the various zones, since it is entirely dependent on latitude. In any case, during much of the summer, day length is essentially the same throughout the entire arctic. Even at latitude 60° north, there are several weeks during which night never falls, although the sun is slightly below the horizon for a few hours out of each twenty-four. It has been shown that most plant species that are sensitive to day length are also sensitive to light intensities of only a fraction of

TABLE 5. FLORISTIC ZONE, *a* VALUE, MEAN ANNUAL TEMPERATURE OF SELECTED ARCTIC AND SUBARCTIC STATIONS

Zone numbers in parentheses indicate that the station is near the boundary of that zone (data from Walter, 1960).

	Station	Zone	*a*°	Mean ann. temp. (°C)
Alaska				
	Barter Island	2 (3)	11	–11.9
	Shishmaref	4	24	–6.6
	Wales	4	28	–5.7
	Saint Michael	4 (subarc.)	33	–3.4
Canada				
	Mould Bay	1 (2)	6	–17.8
	Clyde	3 (2)	12	–12.0
	Pond Inlet	3 (2)	14	–14.1
	Arctic Bay	2 (3)	15	–13.5
	Padloping Island	3	16	–10.3
	Holman Island	3	15.5	–11.7
	Coral Harbor	3 (4)	19	–11.8
	Frobisher Bay	4 (3)	22	–9.0
	Chesterfield Inlet	4	24	–11.8
	Port Harrison	4	25	–7.5
	Port Radium	subarc. (4)	37	–6.8
	Fort Mackenzie	subarc. (4)	36	–5.1
Greenland				
	Danmarkshavn	2	9	–11.4
	Inglefield Bay	2	10	–12.5
	Thule	3 (2)	12	–11.1
	Peary Land	2	14	–15.0
	Scoresbysund	3	16	–6.3
	Umanak	3 (4)	25	–2.8
	Godhavn	4	24	–0.9
	Angmagssalik	4	28	–0.9
	Godthaab	4	31	–0.8
	Kornok	4 (subarc.)	39	–0.6
	Sletten	4 (subarc.)	41	1.6
Jan Mayen Island		3 (4)	19.5	0.0
Bear Island		3	17.5	–5.0
Spitzbergen				
	Quade Hook	2	10.5	–6.7
	Green Harbor	3 (2)	14	–8.0
Iceland				
	Grimsey	4	32	1.6
	Akureyri	4 (subarc.)	41	2.3
	Reykyavik	subarc. (4)	54	3.9
Norway				
	Tromsø	subarc. (4)	42	2.3
	Vardø	4 (subarc.)	35	1.1
	Röst (Lofoten Is.)	subarc. (4)	58	4.7
Franz Josef Land				
	Rudolph	1	1.0	–11.8
European Russia				
	Aleksandrovsk	4 (subarc.)	36	–0.3
	Kola	4 (subarc.)	41	–0.7
	Kanin Nos	4	30	1.1
	Kolgujev I.	4	25	–3.0

TABLE 5 (continued)

	Station	Zone	a^*	Mean ann. temp. (°C)
Novaya Zemlya				
	Cape Shelanija	2 (1)	6	–9.2
	Ruskaya Gavanj	2	8	–6.2
	Matotchkin Shar	2 (3)	12.5	–8.5
	Malyje Karamenkaly	3	17	–6.0
	Varneka Bay (Vaigatch)	3	19	–6.7
Western Siberia				
	Bely I.	2	12	–9.7
	Cape Drovjanov	2	13	–9.9
	Dixon	2	8	–12.7
	Dudinka	4 (subarc.)	31	–10.7
	Igarka	subarc. (4)	41	–8.6
Eastern Siberia				
	Cape Shelagshi	2	12	–12.2
	Uelen	3	14.5	–8.6
	Chatanga	4	26	–13.5
	Bulun	4	27	–14.4
	Anadyr	4	30	–7.9
	Abyj	subarc. (4)	38	–14.4
	Verkoyansk	subarc.	45	–16.1
New Siberian Is.				
	Kotelny I.	1	5	–14.4
	Cape Kigiljaka	2 (1)	6	–14.2
	Liakovsky I.	2 (1)	6.5	–14.7
Okhotsk Region				
	Okhotsk	4 (subarc.)	36	–5.7
Kamtchatka				
	Ust Kamtschatsk	subarctic	45	1.2
Commander Islands				
	Bering I.	4 (subarc.)	42	–1.5

* Aggregate of mean temperatures above O° C.

those of broad daylight (Meyer, Anderson & Böhning 1960). Day length is therefore excluded as a major factor in affecting the distribution of arctic plants.

All zonal soils in arctic regions are generally considered to fall into a single category, arctic brown soils (Tedrow & Cantlon 1958). They are rather uncommon, particularly in the higher arctic regions. Most arctic "soils" are azonal bog soils and lithosols which are so universally distributed throughout the arctic that there is little chance of their affecting plant distribution on a broad scale. None of the floristic zones can be characterized as to soil type or other edaphic features.

Although the floristic zones are correlated with the amount of summer warmth to the point that other ecological factors are insignificant by comparison, not all arctic plants conform to the zones in terms of their northern limit of distribution. In some cases, this can be explained on the basis of ecological factors, other than summer warmth, affecting the northern limit of distribution of certain species and plant groups. This is discussed in the following section.

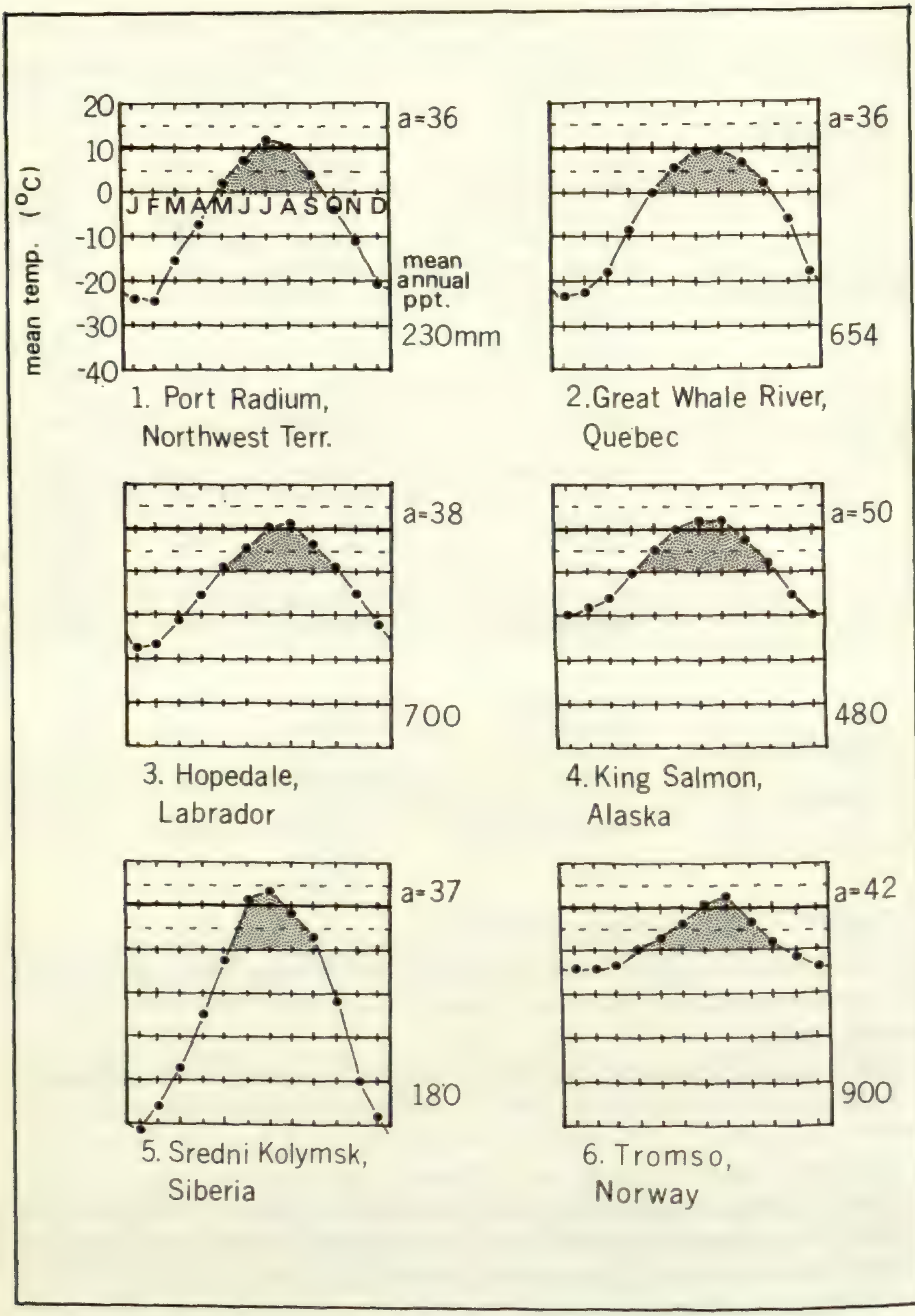


FIG. 19. Climatographs from several stations near arctic timberline, *a* is the aggregate of the mean temperatures of the months with a mean temperature above 0° C. This is equal to the shaded area under the curve. Data mainly from Walter (1960).

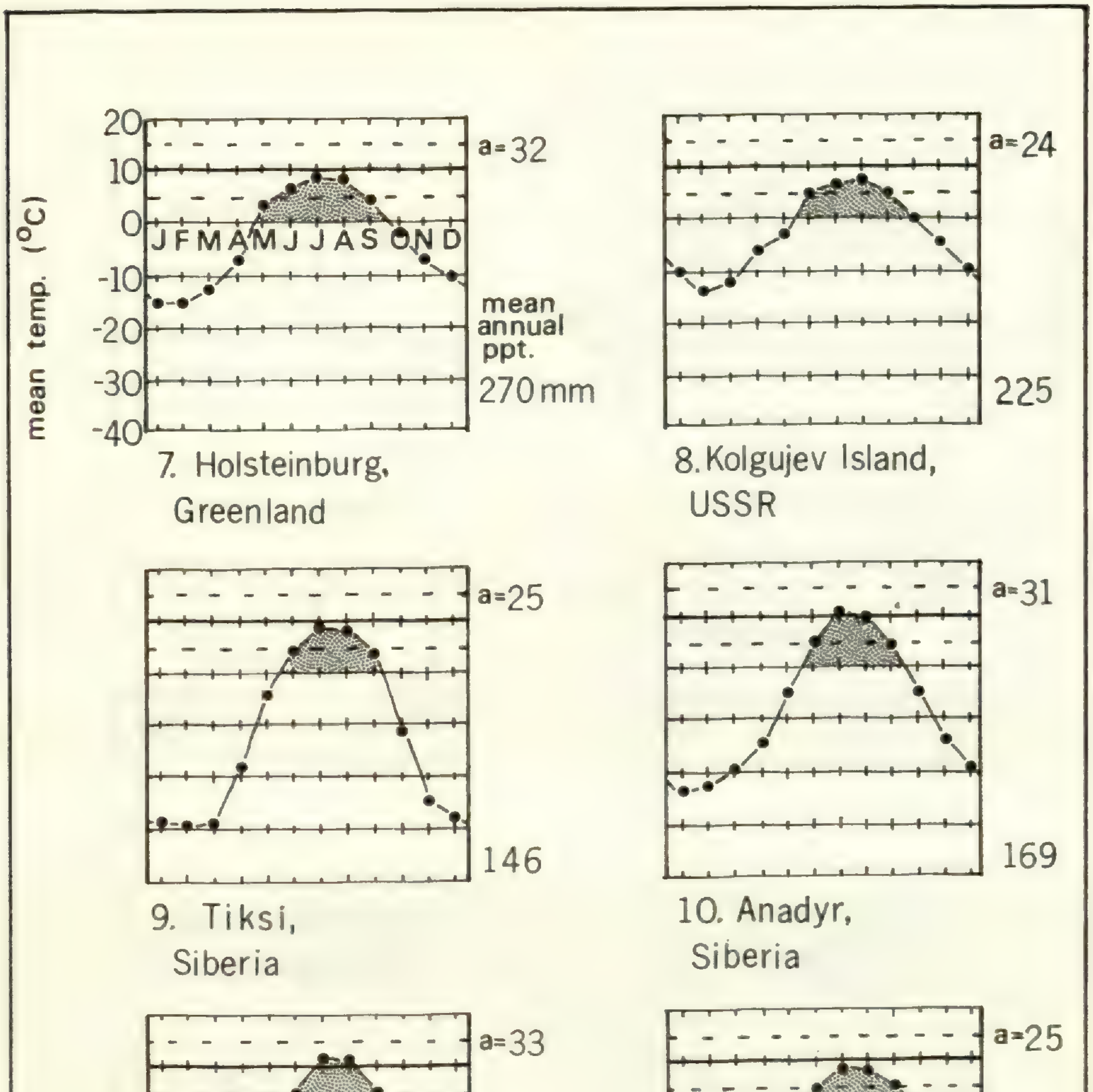


FIG. 20. Climatographs for several stations located in zone 4. Data as for Fig. 19.

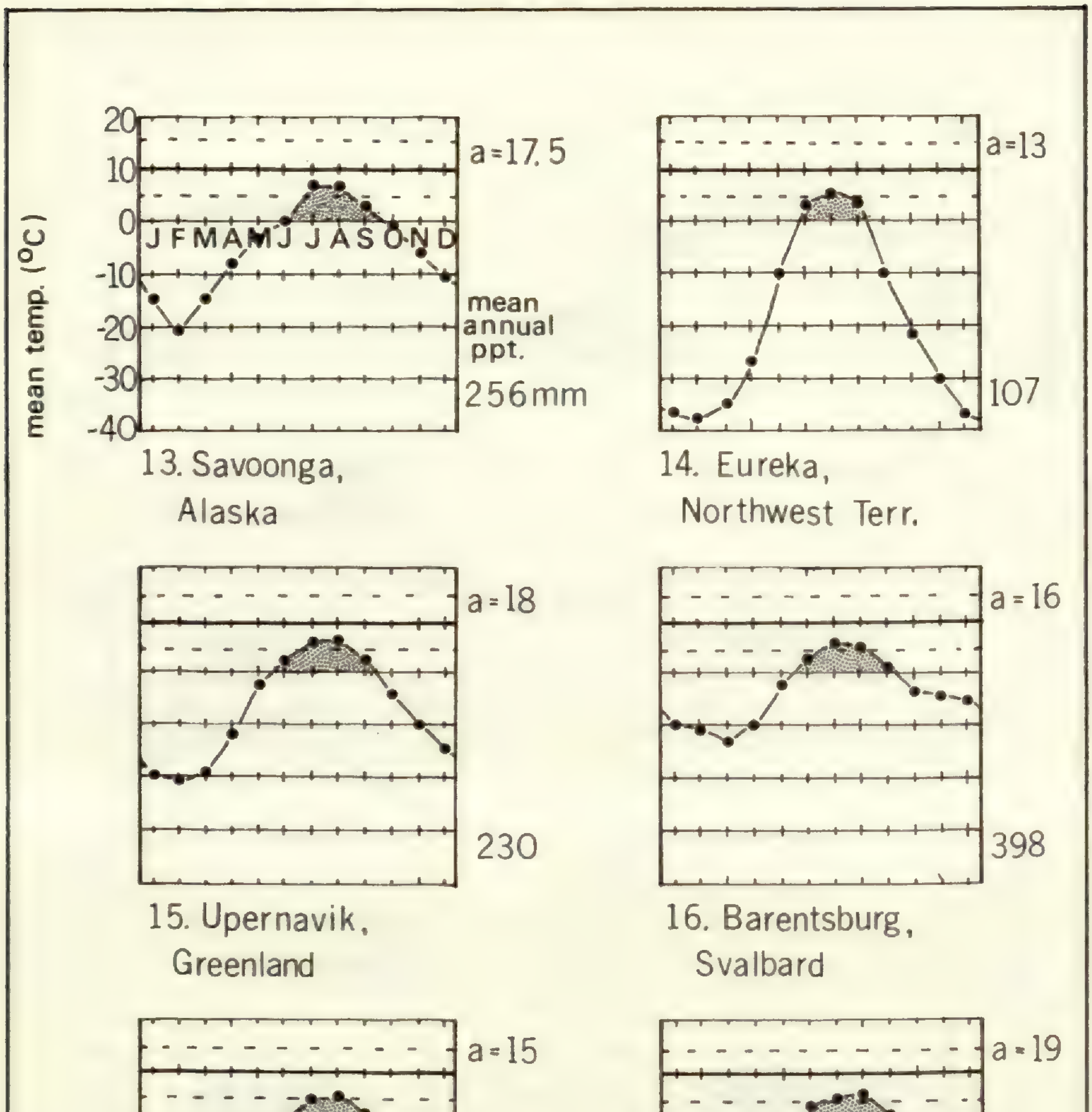


FIG. 21. Climatographs for several stations located in zone 3. Data as for Fig. 19.

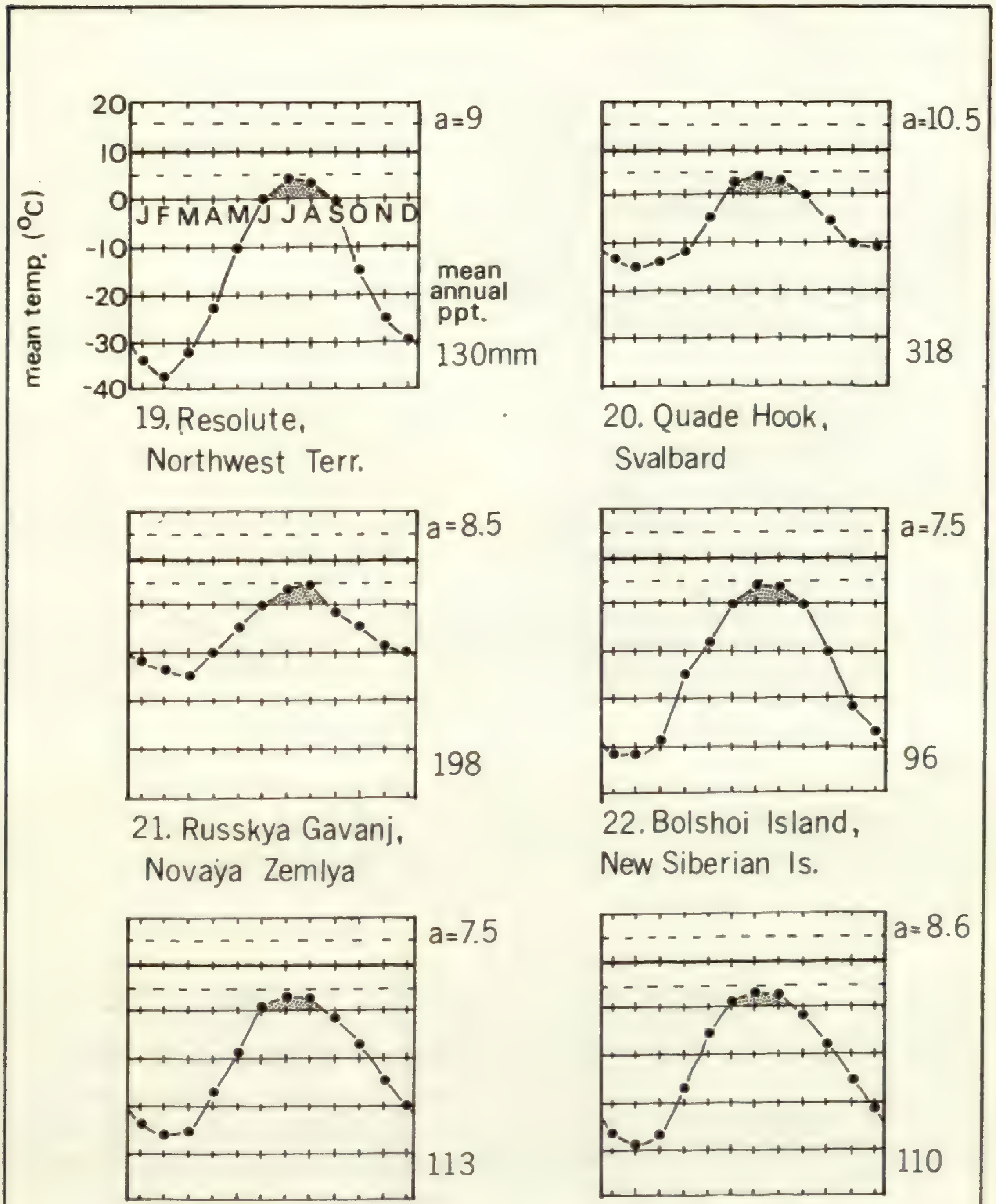


FIG. 22. Climatographs for several stations located in zone 2. Data as in Fig. 19.

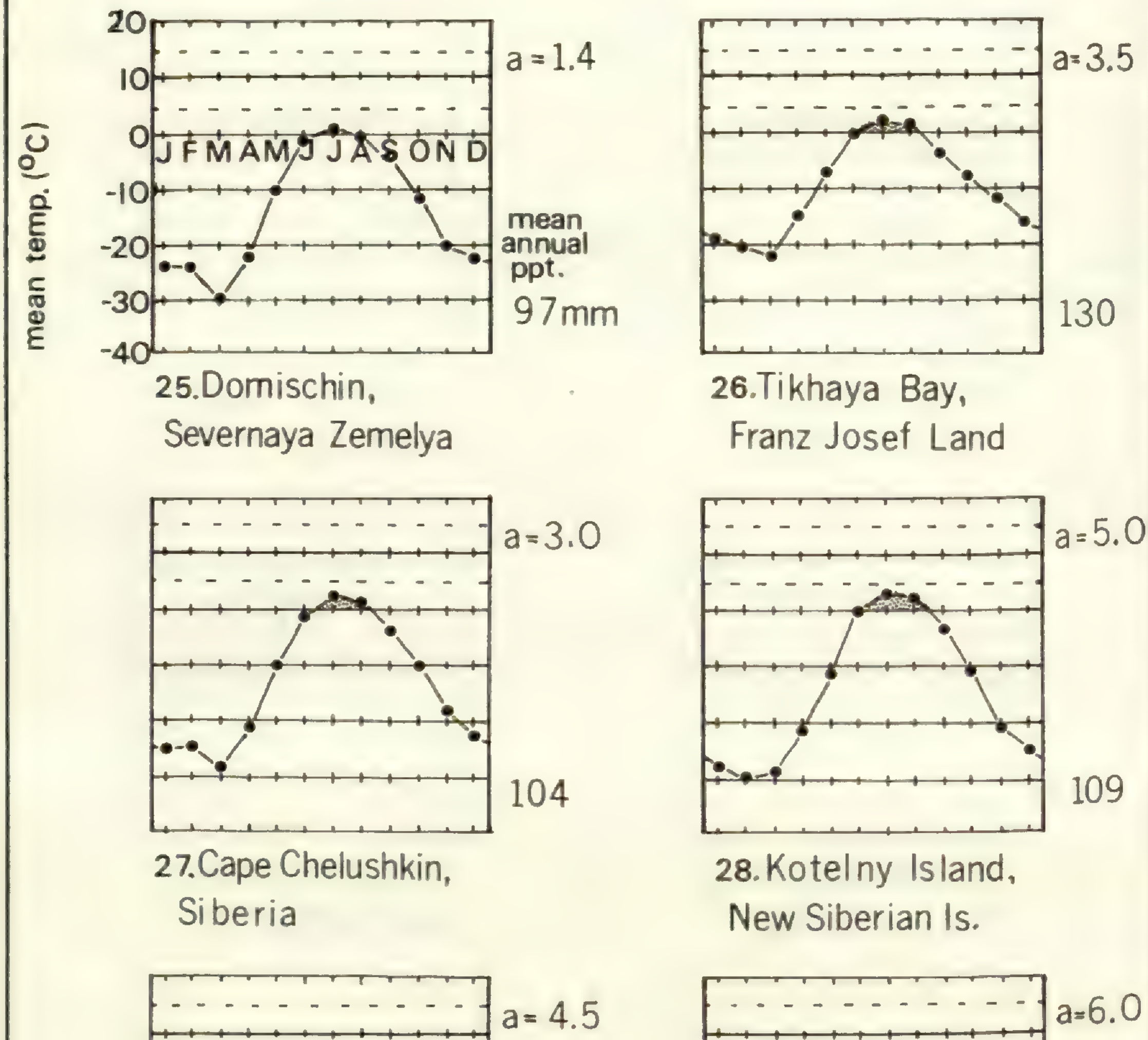


FIG. 23. Climatographs for several stations located in zone 1. Data as in Fig. 19.

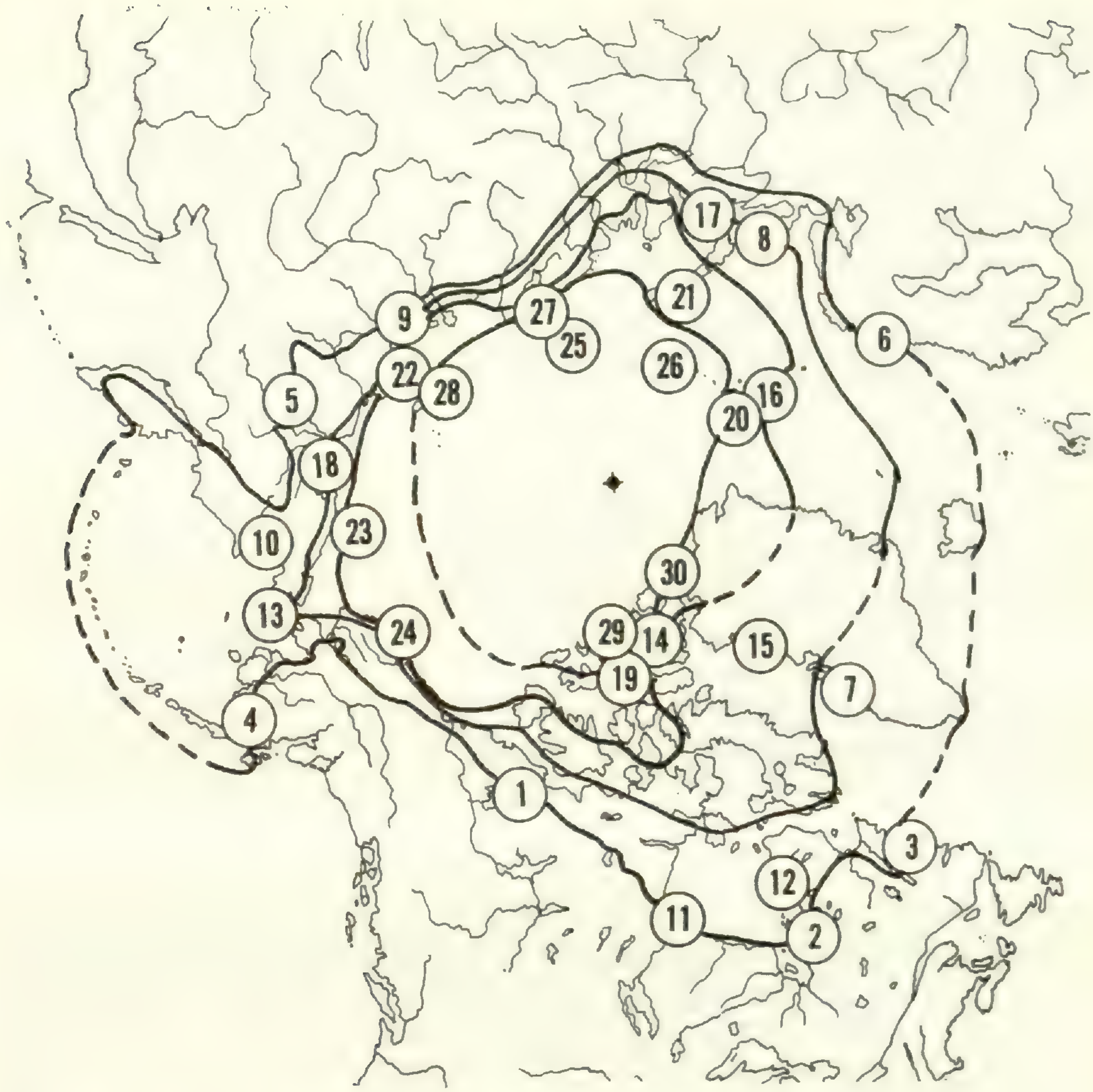


FIG. 24. Map showing locations of the 30 stations treated in Figs. 19–23.

Plants Which Do Not Conform to Zone Boundaries. In terms of habitat preference, three groups of plants have distribution patterns whose ranges are difficult to predict. They are: aquatics, strand plants and alpine species. The last group requires almost perfect drainage, and it should be recalled that alpine conditions can occur at any altitude in arctic regions.

Submersed aquatics are rare in the higher arctic, being virtually absent in zones 1 and 2. In the lower zones, aquatics tend to reverse the normal pattern of extending farther to the north in continental than in maritime areas. Many aquatic species which are normally confined to zone 4 reach well into zone 3 in both East and West Greenland. Many of the same species also occur in insular zone 3 areas such as St. Lawrence Island, Svalbard, and Novaya Zemlya. Examples are *Sparganium hyperboreum, Potamogeton perfoliatus* and *Ranunculus aquatilis.* A similar situation, although not as well marked, occurs with respect to semi-aquatic species such as *Triglochin palustre, Equisetum palustre* and *Eleocharis acicularis.* The explanation for this seeming anomaly is undoubtedly related to ice

conditions. The thickness of the ice and the duration of ice cover must be closely related to winter temperatures and snow cover. Areas with low winter temperatures and light snow cover have a shorter growing season for aquatic plants than do areas with moderate winter temperatures and a heavy snow cover, other factors being equal. The total depth of freezing must also affect the suitability of a pond or lake habitat for aquatic plants. Many aquatic species winter over by means of buds or roots under the ice. Probably few of these could survive in ponds which freeze solid.

The ranges of arctic strand plants vary greatly, but many are similar in having a gap in their distribution along the arctic coast of Siberia, or in arctic Canada. With the exception of these gaps, many strand species conform well to zone boundaries. For example, *Elymus arenarius, Honckenya peploides* and *Mertensia maritima* have quite characteristic upper zone 3 distributions except that they are not known to occur along most of the northern coast of Siberia. The special distribution patterns of strand plants are probably due to two factors. First, their ranges are essentially linear, and the species cannot migrate along a broad front, which slows the populating of new areas. They are more likely to be trapped and eliminated by climatic changes or advancing ice sheets than are terrestrial species. Also, strand plants are subject to physical disturbances by pack ice in much of the arctic. Long stretches of coast line on the Arctic Ocean are probably subject to such intense plowing action by ice each year that strand plants can never become established.

"Alpine" plants do not form as clearly a defined group as aquatics and strand plants, but there are many arctic species which do not colonize areas where there is no significant topographical relief. The necessity for perfect drainage is a major factor in the distribution of these species. Most arctic regions have some mountainous or hilly and rolling terrain, and their floras include a large complement of alpine species. One exception is the northern part of the arctic slope in Alaska, an area about 500 miles long and over 100 miles wide. A large number of species are common throughout much of arctic Alaska, including the Brooks Range and St. Lawrence Island, but are absent from the northern part of the arctic slope. Examples are: *Polygonum bistorta, Anemone narcissiflora, Corydalis pauciflora, Eritrichium* species, *Myosotis alpestris* and *Artemisia glomerata.* Many of the alpine species are known to occur on Wrangel Island in zone 2, and some on the New Siberian Islands in northern zone 2 or even zone 1. Obviously, summer temperature is not an important factor in restricting these species from the arctic slope, most of which lies in zone 4. Other arctic areas with low relief are the Mackenzie Delta area, the Hudson Bay lowlands, the Yamal Peninsula and the northern part of the West Siberian lowlands, and some of the deltas of the major Siberian rivers, such as the Lena and Kolyma. Since several of these areas are where the arctic is reduced to a comparatively narrow coastal strip, it can be seen that these lowlands could act as important barriers to the spread of alpine plants in arctic regions.

Many of the Beringean endemics are alpine species, as are others which are widely distributed in Eurasia, but reach North America only in Alaska. Other alpine species range from eastern Asia to Beringea and down the Rocky Mountains. The richness of the flora of the Beringean region and surrounding areas can be largely attributed to the fact that these areas were unglaciated during the Pleistocene and served as refugia for the arctic biota (Hultén 1937). Supposedly, many of the Beringean species formerly had a larger, possibly circumpolar, distribution but they have not recolonized all the areas from which they were eliminated during the glacial advances.

It can also be hypothesized that many of the Beringean endemics and amphi-Beringean species do not have relict ranges; instead, they may be viewed as alpine species which originated in the great mountain complexes of central Asia and western North America. Both of these areas are connected to the Beringean region by continuous ranges of mountains which may be considered migration routes for alpine plants. However, from the Beringean region to other parts of the arctic these routes are blocked by lowland areas which are inhospitable to alpine plants, so that many of the Beringean alpine plants have not been able to colonize other alpine areas in the arctic. Thus, the present distribution of the Beringean plants may depend as much or more on currently acting ecological factors as on historical factors.

In terms of distribution patterns, two groups of widely distributed species, whose northern limits of distribution do not conform well with the floristic zones, may be distinguished. One consists of species having a greater or lesser gap in an otherwise circumpolar range, but whose northern range limits conform well to the zone boundaries. The majority of species whose range is less than circumpolar belong to this group. Examples are *Campanula uniflora* and *Dryas integrifolia*. *Campanula uniflora* is not known throughout most of Siberia, but in all other parts of the arctic its northern limit is slightly north of the zone 2-zone 3 boundary. *Dryas integrifolia* is almost entirely confined to the North American arctic, but its northern limit there is almost exactly the zone 1-zone 2 boundary (Fig. 6). In Eurasia, *D. integrifolia* is replaced by the related but distinct *D. octopetala* (often treated as several related species, Porsild 1947). Where *D. octopetala* and *D. integrifolia* come in contact in North America, their habitat preferences differ, and they seldom hydridize. *Dryas octopetala* conforms almost perfectly to the zone 1-zone 2 boundary in Eurasia as does *D. integrifolia* in North America. A similar situation occurs in a number of other circumpolar complexes—for example, in the *Cerastium arcticum* group, the *Poa arctica* group, and in parts of the genera *Melandrium* and *Pedicularis*. This indicates that plants tend to be conservative with respect to their requirements for a critical amount of summer warmth. The ability of a species to expand its range northward beyond a certain limit is usually not subject to much geographic variation.

The species in the group mentioned above do not constitute an exception

to the theory of floristic zonation and its relationship to amounts of available summer warmth. These species have not attained a circumpolar range either because of historical or distributional factors, or because of the existence of replacement species in other parts of the range, but they still conform to zone boundaries throughout their ranges.

However, there are a few cases in which a widespread, even circumpolar, species has a different northern limit in different sectors of its range. *Rubus chamaemorus* is a zone 3 species in most of the arctic, but it only reaches the southern tip of Greenland. *Caltha palustris* is a zone 2 species throughout Eurasia and western North America, but in the rest of North America it is a low arctic or subarctic species, not reaching Baffin Island or Greenland. *Lathyrus japonica* occurs in zone 2 and is common in zone 3 in the Beringean-Chukchi Sea region, but barely reaches zone 4 in Greenland, Labrador and western USSR.

When a species has an anomalous distribution of this type, one of three explanations is possible. First, the distribution of the species may be controlled by a factor other than summer warmth, as has already been considered in the case of aquatics, strand plants and "alpine" plants. Second, the taxonomy of the group may be imperfectly understood, and a group treated as a single taxon may, in fact, include two taxa which are morphologically similar, but with different physiological characteristics. Finally, the anomaly may be due to historical and geographical factors, in the sense that the species under discussion have not become established throughout their potential range.

There is no rule regarding which explanation, or which combination, applies in a given case. However, a few points can be made: first, one should determine whether the range of the species under consideration is unique, or whether there is a group of species with a similar distribution pattern. If it is found that several species share the same distributional pattern, the next step is to decide whether the species are related taxonomically or ecologically, or whether the only relationship is similarity of the ranges. If the group of species has a specialized habitat requirement, it is probable that this is the main factor causing the anomalous distribution pattern. This has been discussed under aquatic plants above. If the group is taxonomically related, the anomalous distribution pattern may be due either to historical factors or to specialized requirements of the members of the taxon involved. If the group to which the species belongs has a major center of radiation which is presently evident, it can be concluded that the group is probably relatively young, rapidly evolving and has not yet fulfilled its potential range. Thus the anomalous distribution patterns are probably largely related to historical factors. Good examples are the genera *Pedicularis* and *Primula*. Both of these have centers of radiation in the mountains of eastern Asia, and their arctic representatives tend to be clustered in the Beringean region. There is little doubt that many species of these genera have only recently

migrated to the arctic and they can be expected to increase their range in the future.

But if the taxonomically related species with anomalous distribution patterns belong to more or less uniformly distributed groups, it may be that the anomalies are related to some unique physiological feature of the group. It is difficult to apply experimental evidence to this problem, and there are no examples of such a situation. It is interesting to note that a number of genera of *Umbelliferae* that are normally not found north of the temperate zone occur commonly in arctic parts of the Beringean region, indicating that perhaps many *Umbelliferae* find some necessary but unknown habitat requirements in the Beringean region.

If the group of species under discussion shows no relationship, either in terms of habitat requirements or taxonomy, then it is reasonable to conclude that historical factors are responsible for the distribution pattern.

On the Physiological Effects of Low Amounts of Summer Warmth

There is an important correlation between the northern limits of the ranges of arctic plants and the amount of warmth available during the summer. However, there is virtually no direct evidence regarding the cause. It is well-known that temperatures (and other climatic factors) vary considerably between the immediate environment of arctic and alpine plants and the altitude at which temperature readings are commonly taken (cf., Bliss 1962). Therefore, the correlation between *a* and the northern limit of a given species is not direct, but depends on an assumed correlation between *a* and a critical amount of warmth available to the plant.

The actual physiological responses of plants to critical amounts of warmth are unknown and will continue to be so until laboratory experiments on the physiology of the plants in question have been carried out. However, field observations indicate that there are certain concepts and lines of investigation which should prove fruitful. We can hypothesize that the reproductive phase of the life cycle of a plant is the most sensitive to critically low amounts of warmth, either in the production of propagules or their germination. Obviously, a species cannot be considered fully established in an area unless it is capable of completing the entire reproductive cycle. However, individual invaders, capable of completing the germination phase only, could persist in quantity, depending on the number of propagules arriving at the area in question, and the life span of the plants.

There are examples, in the St. Lawrence Island flora, of species which can be found in quantity in certain locations, but field observations indicate that they do not normally produce viable seeds or other propagules. *Lycopodium clavatum, Epilobium angustifolium* and *Linnaea borealis,* although each is known to occur at several stations on St. Lawrence, have not been observed to produce any reproductive structures

but their vegetative growth is apparently normal. Other species produce normal appearing flowers, but were never observed to set fruit. *Rubus arcticus* and *Cornus suecica* are examples. These species are usually found in rather large but rare and widely scattered colonies, each of which is probably a clone resulting from the germination of a single propagule originating on some mainland area. Of particular interest is *Potentilla palustris*. This species is fairly common in tundra pools over most of St. Lawrence, but it has been observed in flower only along a few river banks on the south side of the island. Apparently conditions here are near the critical limit for its reproduction. Propagules from the few reproductive stations on St. Lawrence or from the mainland probably are spread to other parts of the island by waterfowl. The peripheral populations of *P. palustris* survive only because of an influx of propagules from an outside source, or perhaps because of a long life span.

Although tundra vegetation is of low and predominately herbaceous growth, it is evident that the life spans of individual tundra plants and clones are often very long. There is little direct evidence regarding the life span of the tundra plants, but it seems appropriate to consider the tundra vegetation as being a dwarf forest, rather than as an assemblage of short-lived annuals and perennials. Of the 238 species known to occur on St. Lawrence Island, only two, *Koenigia islandica* and *Montia fontana,* are true annuals. The only known colony of *Dryas integrifolia* on the island is almost certainly the one from which Chamisso collected specimens in 1816. We can only speculate on the life span of a clump of plants of a given species such as *Carex aquatilis,* but there can be little doubt that it is measured in tens if not hundreds of years.

The long life span of many tundra plants means that there is no necessity for them to be able to reproduce every year. It is possible that many of the species could actively extend their range into areas where conditions allowed sexual reproduction (or other reproduction which produced dispersible propagules) to take place only once in a decade or even less. Therefore, it appears that if the ability to produce propagules is the main barrier to be crossed by a species in becoming established in a new arctic area, and if this ability is combined with a critical amount of warmth during the growing season, then the operating factor is not necessarily the mean amount of warmth over a period of years, but the likelihood that the critical amount of warmth necessary for the production of propagules will be reached during one or more growing seasons during the life of the plant.

A similar situation would occur in the case of a species whose barrier was the germination of the propagule. Here, the probability of the propagule establishing itself would depend on a combination of the propagule landing in the target area, and conditions for germination being met during a given year. A third factor, of course, would be the length of time the propagule could remain alive but dormant until the proper conditions were available. This offers a reasonable explanation for the presence, on

St. Lawrence, of a number of zone 4 species. The close proximity of the island to a good source of propagules of zone 4 species makes it likely that they will be available when the conditions necessary for germination occur. Isolated zone 3 areas, such as those of Spitzbergen and Ellesmere Island, would have little likelihood of having viable propagules of marginal species available when conditions were suitable for germination.

If the factors that limit the establishment of arctic plants beyond their ranges are a matter of exceptional, rather than average, conditions, does this invalidate the concept that the presence or absence of a given species in a given area can be predicted on the basis of *a*, a figure derived from mean values? We can only say that the correlation between *a* values and the ranges of arctic plants is demonstrably significant. If exceptional conditions govern the ranges of species, then average conditions, as exemplified by *a*, offer a good index of the probability that the required exceptional conditions will occur often enough to allow species to become established in a given area.

Some Implications of Floristic Zonation in the Arctic

Since the floristic zone to which an area belongs is correlated with a rather specific amount of summer warmth, if the zone to which an area belongs is known, a reasonable estimate can be made of the summer temperature regime of an area.

For example, Jan Mayen Island, which lies at about 72° N off the east coast of Greenland, supports a depauperate flora consisting of 62 species. This estimate is based on the rather liberal treatment of Lid (1964). Therefore, it might be expected that the island would fall into one of the higher arctic zones, perhaps upper zone 2. However, the Jan Mayen flora contains a number of species that are definitely not typical of upper zone 2. *Carex Lachenalii, Luzula arcuata, Honckenya peploides, Cassiope hypnoides, Empetrum nigrum* and *Mertensia maritima* are definitely species of zone 3, while *Sibbaldia procumbens, Epilobium anagallidifolium* and *Veronica alpina* are basically zone 4 species which barely reach zone 3. Therefore, we must conclude that Jan Mayen is a zone 3 area, and that the presence of a few species which reach only the lower edge of zone 3 indicates that the island is near the border between zones 4 and 3. The depauperateness of the flora is related to isolation, not climate. Because the aggregate of mean monthly temperatures above freezing for zone 3 areas usually lies between 12° and 20° C, we should expect the figure for Jan Mayen to be near 20° C. The island is obviously subject to a maritime climate, therefore we may expect that the highest mean monthly temperatures will occur in August rather than in July, that it will be comparatively low for a zone 3 area, and that the period of time during which temperatures average above freezing will be comparatively long.

Climatic data from Jan Mayen (Walter 1960) show that the prediction made above is quite accurate. The mean monthly temperature for the

warm months is as follows: May 0° C; June 3°; July 5°; August 6.5°; September 4°; October 1°. The aggregate temperature (a) is therefore 19.5° C.

It is remarkable how accurate an estimate of the summer temperature regime can be made on the basis of floristic data. The close agreement between the predicted and observed temperatures on Jan Mayen indicates that accurate predictions can be made even on the basis of a small and abnormally depauperate flora. One might expect that a similar prediction could be made in the case of a Pleistocene or Recent fossil flora even though the species represented in a fossil flora may be only a fraction of those present in the original flora.

In practice, there are two difficulties involved in making predictions of this sort. The first is that most fossil floras known from the Pleistocene in the arctic are known from pollen studies. Pollen is often identifiable only to the generic level, and relatively few of the common genera in the arctic flora are of much use in defining zone boundaries unless the exact species is known. Therefore, predictions would often be based on minor elements in a pollen flora, sometimes without considering that rare pollen grains might have been blown in from another area or been redeposited from older strata. To make an accurate estimate of the zone to which an ancient flora belongs, one should really have the actual remains of plant bodies. The second difficulty is that the lowest zone to which the flora could belong cannot be determined with certainty using only a small portion of a flora. The presence of several zone 3 species in a fossil flora indicates that the flora must have been in a zone no higher in the arctic than zone 3, but it does not prove that the flora may not have been a typical zone 4 flora.

In spite of these difficulties, preliminary studies indicate that the correlation of fossil floras with the zones proposed in this paper is possible in some cases. There also seems to be good reason to believe that in many areas the identifiable remains of plants may be recovered from permanently frozen ground. With fossil floras of this type, the major difficulties which arise when only pollen is studied are not applicable.

Distribution patterns which superficially appear to be anomalous and for which complicated historical explanations have been proposed are often easily understood when the concept of zonation is applied. The St. Lawrence Island flora is a good example. One would be hard put to find a good historical explanation for the depauperateness of the flora, but the situation is readily comprehended when it is realized that St. Lawrence is in a different floristic zone than the adjacent mainland. A complementary example is in the flora of the Svalbard archipelago. Svalbard is an isolated group of islands lying between 75° and 80° N. Nearly all of the several land areas are presently glaciated. Nevertheless, the Svalbard archipelago supports a vascular flora of 155 to 160 species (Rönning *in* Löve & Löve 1963). Nearly all of these occur in the relatively

small area in West Spitzbergen known as the Inner Fjord District, and many occurring there are not known elsewhere in the archipelago.

The rich flora of the Inner Fjord District is in sharp contrast to the poor flora of such nearby areas as Franz Josef Land, which, as mentioned above, supports only 36 species. Because of its richness, it has often been suggested that the flora of Svalbard is largely a relict flora, and that unglaciated refugia must have existed there at least during the last glacial period of the Pleistocene. However, it is difficult to understand how this could have been the case, for even at the present time some 90 per cent of the land area of the Archipelago is covered by glacier ice.

An examination of the composition of the flora of Svalbard shows that most of the archipelago supports a typical zone 2 flora which includes some 100 species. The Inner Fjord District supports some 50 additional species. The vast majority of these are zone 3 species, many having typical circumpolar ranges, although in Svalbard they are confined to one small area. In short, the Inner Fjord District is simply a small "island" of zone 3 which is more or less surrounded by zone 2. It will be noted that the summer temperature regime for Barentsberg, Svalbard is exactly what could be expected in a zone 3 area, and is, in fact, similar to that of St. Lawrence Island. The rich flora of the Inner Fjord District is not at all anomalous when compared to other zone 3 areas, and there is no need to propose a theory involving an unglaciated refugium in the area to explain the situation. The only historical aspect of the situation is that the flora is somewhat more depauperate than many other zone 3 floras, which is easily understandable in view of the isolation of the area and the probability that it has recently been glaciated.

LITERATURE CITED

Abbe, E., 1948. *Braya* in Boreal Eastern America. Rhodora **50**: 1–15.

Benson, L., 1948. A Treatise on the North American *Ranunculi*. Amer. Midl. Nat. **40**: 1–261.

————————, 1954. Supplement to a Treatise on the North American *Ranunculi*. Amer. Midl. Nat. **52**: 328–369.

Bliss, L. C., 1962. Adaptations of Arctic and Alpine Plants to Environmental Conditions. Arctic **15**: 117–144.

Böcher, T. W., 1956. Further Studies in *Braya humilis* and Allied Species. Meddel. om Grønland **124** (7): 1–29.

Bowden, W. M., 1957. Cytotaxonomy of Section *Psammelymus* of the Genus *Elymus*. Can. Journ. Bot. **35**: 951–993.

Chamisso, A. L. v., and D. F. L. Schlechtendal, 1826–1836. De Plantis in Expeditione Speculatoria Romanzoffiana Observatis. Linnea 1–10.

Chaney, R. W., 1951. A Revision of Fossil *Sequoia* and *Taxodium* in Western North America Based on the Recent Discovery of *Metasequoia*. Trans. Am. Phil. Soc. II. (40): 169–239.

Colinvaux, P. A., 1964. The Environment of the Bering Land Bridge. Ecol. Monog. **34**: 297–329.

————————, 1967. A Long Pollen Record from Saint Lawrence Island, Bering Sea (Alaska). Paleogeog., Paleoclimatol., Paleoecol., 3: 29–48.

Cronquist, A., 1946. Notes on the *Compositae* of the Northeastern United States. III. *Inuleae* and *Senecioneae*. Rhodora **48**: 116–125.

DAVIDSON, J. F., 1950. The Genus *Polemonium* (Tournefort) L. Univ. Calif. Publ. Bot. **23**: 209–282.
DAVIS, R. J., 1966. The North American Perennial Species of *Claytonia*. Brittonia **18**: 285–303.
DREW, J. V., AND J. C. F. TEDROW, 1962. Arctic Soil Classification and Patterned Ground. Arctic **15**: 109–116.
FLINT, R. F., 1957. Glacial and Pleistocene Geology. New York, Wiley: 553 pp.
GIDDINGS, J. L., 1967. Ancient Men of the Arctic. New York, Knopf: 391 pp.
HANNSEN, O., AND J. LID, 1932. Flowering Plants of Franz Josef Land. Skrifter om Svalgard og Ishavet **39**: 1–42.
HOLM, T., 1907. The Genus *Carex* in North-West America. Bot. Centralbl. Beih. **22** (2): 1–29.
HOPKINS, D. M., 1959a. Cenozoic History of the Bering Land Bridge. Science **129**: 1519–1528.
————————, 1959b. Some Characteristics of the Climate in Forest and Tundra Regions in Alaska. Arctic **12**: 215–220.
————————, (ed.), 1967. The Bering Land Bridge. Stanford: 495 pp.
————————, F. MACNEILL, R. MERKLIN, AND O. PETROV, 1964. Quaternary Correlations Across the Bering Sea. Science **147**: 1107–1114.
————————, AND T. EINARSSON, 1966. Pleistocene Glaciation on St. George, Pribilov Islands. Science **152**: 343–344.
HULTÉN, E., 1937. Outline of the History of Arctic and Boreal Biota During the Quaternary Period. Stockholm: 198 pp.
————————, 1940. History of Botanical Exploration in Alaska and Yukon Territories From the Time of Their Discovery to 1940. Bot. Not. (1940): 289–346.
————————, 1941–1950. Flora of Alaska and the Yukon. Lunds Univ. Arsskr. N.F. Ave. 2, 1941, Bd. 37 (Pt. 1) pp. 3–127; 1942 Bd. 38 (Pt. 2) pp. 131–412; 1943, Bd. 39 (Pt. 3) pp. 415–567; 1944 Bd. 40 (Pt. 4) pp. 571–795; 1945 Bd. 41 (Pt. 5) pp. 799–978; 1946 Bd. 42 (Pt. 6) pp. 981–1066; 1947 Bd. 43 (Pt. 7) pp. 1069–1200; 1948 Bd. 44 (Pt. 8) pp. 1203–1341; 1949 Bd. 45 (Pt. 9) pp. 1345–1481; 1950 Bd. 46 (Pt. 10) pp. 1485–1902.
————————, 1956. The *Cerastium alpinum* Complex. A Case of World-wide Introgressive Hybridization. Svensk. Bot. Tidskr. **50**: 411–495.
————————, 1958. The Amphi-Atlantic Plants. Stockholm: 340 pp.
————————, 1959. The *Trisetum spicatum* Complex. *Trisetum spicatum* (L.) Richt. An Arctic-montane Species With a World-wide Range. Svensk Bot. Tidskr. **53**: 203–228.
————————, 1960. Flora of the Aleutian Islands. J. Cramer, Weinheim/Berggstr.: 376 pp.
————————, 1961. Two *Pedicularis* Species from N.W. America, *P. albertae n. sp.* and *P. sudetica s. lat.* Svensk. Bot. Tidskr. **55**: 193–204.
————————, 1962. The Circumpolar Plants I. Stockholm: 275 pp.
————————, 1968a. Flora of Alaska and Neighboring Territories. Stanford: 1008 pp.
————————, 1968b. Comments on the Flora of Alaska and Yukon. Arkiv. för Botanik **7**: 1–147.
HUSTICH, I., 1953. The Boreal Limit of Conifers. Arctic **6**: 149–162.
JOHANSEN, F., 1924. Report on the Canadian Arctic Expedition 1913–1918. Vol. 5, part C: 1c–86c.
JOHNSON, A. W., L. A. VIERECK, R. E. JOHNSON, AND H. MELCHIOR, 1966. Vegetation and Flora, pp. 277–354 *in* Wilimovsky, ed., Environment of the Cape Thompson Region, Alaska: U.S. Atomic Energy Comm. Pub. PNE–481.
JUZCEPZUK, S. V., 1929. Beitrage zur Systematik der Gattung *Dryas*. Bull. Jard. Bot. Princip. de l'URSS **28**: 306–327.
KIMBLE, G. AND D. GOOD, 1955. Geography of the Northlands. Am. Geog. Soc. Special Pub. 32. 534 pp.
KJELLMAN, F. R., 1882. Fanerogamfloran pa. St. Lawrnece-ön. Vega Expeditions Vetenskapliga Iakttagelser: 1–23.
KOEPPEN, W., 1936. Das Geographische System der Klimate. *In* Handbuch der Klimatologie, Koeppen and R. Geiger eds. Berlin: 636 pp.

KÜKENTHAL, G., 1909. *Cyperaceae-Caricoideae. In* Engler, Das Pflanzenreich IV. 20.
LID, J., 1964. The Flora of Jan Mayan. Skrifter om Svalbard og Ishavet **130:** 1–109.
LÖVE, A. AND D. LÖVE (eds.), 1963. North Atlantic Biota and their History. New York: 430 pp.
MACKENZIE, K. K., 1941. Keys to the North America Species of *Carex*. New York Bot. Garden: 80 pp.
MEINSHAUSEN, K. F., 1900. Der *Cyperaceen* der Flora Russlands. Acta Horti Petrop. **18:** 221–415.
MERRIAM, C. H., 1894. Laws of Temperature Control of the Geographic Distribution of Terrestrial Animals and Plants. Nat. Geog. Mag. **6:** 229–238.
MEYER, B. S., D. B. ANDERSON, AND R. H. BÖHNING, 1960. Introduction to Plant Physiology. Princeton: 541 pp.
MUIR, J., 1918. Some Botanical Notes From the Cruise of the *Corwin*. Torreya **18:** 197–210.
NORDENSKJÖLD, O. AND L. MECKLING, 1928. The Geography of the Polar Regions. Am. Geog. Soc. Spec. Pub. No. 8, 1–359.
POLUNIN, N., 1959. Circumpolar Arctic Flora. Oxford: 514 pp.
PORSILD, A. E., 1947. The Genus *Dryas* in North America. Canad. Field Nat. **61:** 175–192.
————————, 1954. The North American Races of *Saxifraga flagellaris*. Willd. Bot. Tidskr. **51:** 292–299.
————————, 1964. Illustrated Flora of the Canadian Arctic Archipelago. Nat. Mus. Canada Bull.
————————, 1965. Some New or Critical Vascular Plants of Alaska and Yukon. Canad. Field Nat. **79:** 79–90.
RAUP, H. M., 1959. The Willows of Boreal Western America. Contr. Gray Herb. CLXXXV: 3–95.
RAY, D. J., 1961. Artists of the Tundra and the Sea. Seattle: 170 pp.
ROLLINS, R. C., 1953. *Braya* in Colorado. Rhodora **55:** 109–116.
SAVILLE, D. B. O., 1961. The Botany of the Northern Queen Elizabeth Islands. Can. Journ. Bot. **39:** 909–942.
SCHOLANDER, P. F., 1934. Vascular Plants from Northern Svalbard. Skrifter om Svalbard og Ishavet **62:** 1–155.
SIMPSON, G. G., 1940. Mammals and Land Bridges. Journ. Washington Acad. Sci. **30:** 137–163.
SØRENSON, T., 1953. A Revision of the Greenland Species of *Puccinellia* Parl. Meddel. om Grønland **136**(3): 1–179.
TEDROW, J. C. F. AND J. E. CANTLON, 1958. Concepts of Soil Formation and Classification in Arctic Regions. Arctic 11: 166–179.
TOLMATCHEV, A. I., 1936. Obzor Flory Novoi Zemli. Arctica **4:** 143–178.
————————, 1960–1966. Flora Arctica URRS. 1960: I: *Polypodiaceae-Butomaceae*. Moscow: 101 pp. 1963: IV: *Lemnaceae-Orchidaceae*. Moscow: 95 pp. 1964: II: *Gramineae*. Moscow: 272 pp. 1966: III: *Cyperaceae*. Moscow: 174 pp. 1966b: V: *Salicaceae-Portulacaceae*. Moscow: 207 pp.
WALTER, H., 1960. Klimadiagram Weltatlas. Gustav Fischer, Jena.
WIGGINS, I., AND J. H. THOMAS, 1962. A Flora of the Alaskan Arctic Slope. Toronto: 425 pp.
YOUNG, S. B., On the Taxonomy of *Vaccinium uliginosum* L. In press: Rhodora.
———————— AND E. HALL, 1969. Contributions to the Ethnobotany of Saint Lawrence Island. Anthropological papers of the University of Alaska.

CHROMOSOME NUMBERS OF CRUCIFERAE. II.[1]

REED C. ROLLINS AND LILY RÜDENBERG

Along with general taxonomic research on the *Cruciferae* of the Western Hemisphere and more intensive revisionary studies of particular genera, a continuous program of chromosome counting and breeding system testing has been underway for some years. In many cases, seeds have been obtained from wild sources and plants were grown in the greenhouse to provide either root-tips or flowering buds for chromosome counting. Otherwise, fixations of bud material have been made in the field. The distinction between greenhouse collections and field collections is made where the data are presented. In all instances, voucher specimens were prepared and deposited in the Gray Herbarium.

The most significant immediate problem in which chromosome number information is helping to establish a measure of understanding concerns certain taxonomically complex species groups of *Arabis*. The initial breakthrough came from the work of Böcher (1951) in which he established the presence of apomixis in the genus. In subsequent studies (Böcher 1954, 1969), evidence for widespread apomixis in *Arabis* was increased and the frequent association of asymmetrical chromosome numbers with apomixis was established. Facultative apomixis appears to be the rule. Previous studies by one of us (Rollins 1941, 1966) support the general assumption that several agamic complexes exist in the genus. The additional chromosome counts presented below further add to the overall evidence for this assumption.

In the following lists, the somatic counts from root-tips, or occasionally from some other somatic cell, are given as $2n$, and those from pollen mother cells or immature pollen grains (microsporocytes) as n.

Arabidella

A. trisecta (F. Muell.) O. E. Schultz

$n = 12$: plants from seeds of D. J. E. Whitley 2490. Far northeastern South Australia.

To our knowledge, this is the first report of a chromosome count in the genus *Arabidella*.

Arabis

A. breweri Watson var. *breweri*

$2n = 14$: plants from seeds of Heckard, Constance & Ornduff 2319, Shasta Co., California.

[1] The first paper in this series was published in Contrib. Gray Herb. CXCVII: 43–65. 1966. Some of the field work involved in this research was supported by funds from National Science Foundation Grant GB5872 to the senior author.

A. constancei Rollins

$2n = 14$: plants from seeds of Constance & Chuang 3875, Plumas Co., California.

A. holboellii Hornem. var. *pinetorum* (Tidestr.) Rollins

$2n = 21 \pm 1$: plants from seeds of Constance & Chuang 3876, Plumas Co., California.

A. inyoensis Rollins

$2n = 21$: plants from seeds of Reveal & Beatley 1475, Lincoln Co., Nevada. Plate I, fig. 1.

$2n = 23$: plants from seeds of Beatley 9454, Nye Co., Nevada.

A. perennans Watson

$n = 7$: Coconino Co., Arizona, Rollins 6765.

A. pulchra Jones var. *pulchra*

$2n = 14$: Kane Co., Utah, Rollins 6786.

A. pulchra Jones var. *munciensis* Jones

$2n = 21$: plants from seeds of Beatley & Bostick 4048, Nye Co., Nevada. Plate I, fig. 2, fig. 4.

A. pulchra Jones var. *gracilis* Jones

$2n = 21$: plants from seeds of Beatley 8829, Nye Co., Nevada.

A. sparsiflora Nuttall var. *subvillosa* (Wats.) Rollins

$2n = 21$, $2n = 21 + 1B$, $2n = 22$: plants from seeds of Al-Shehbaz 6950, Siskiyou Co., California. Plate I, fig. 3.

Arabis breweri is in the *A. sparsiflora* complex of species in which Böcher (1969) has reported evidence of apomixis. The chromsome numbers of the group as a whole seem to be based on $n = 7$ to which *A. breweri* conforms. Many of the populations of *A. breweri* appear to be relatively stable morphologically. The plants studied are of this sort and the chromosome number is uniform. In contrast, the cytological picture in *A. sparsiflora* var. *subvillosa* is very suggestive of an apomictic situation and helps to strengthen the evidence that apomixis is present and perhaps even widespread in *A. sparsiflora*. Surprisingly few chromosome counts have been published for *A. sparsiflora* when one considers the great abundance of plants and wide distribution of the species. Raven *et al.* (1965) published $n = 22$ for *A. sparsiflora* var. *californica*, and Böcher (*loc. cit.*) reported $2n = 23$ for *A. sparsiflora* var. *atrorubens* and the same number for *A. sparsiflora* var. *columbiana*. Although these numbers deviate slightly from an exact multiple of $n = 7$, as do some of our counts, it is clear that an agamic complex, such as this seems to be, can readily accomodate such deviating and asymmetric numbers.

Our most recent count of $2n = 21 \pm 1$ for *A. holboelii* var. *pinetorum* on California material along with previous counts of $2n = 21$ on plants from Wyoming (Rollins 1966) and $n = 14$ and $n = 21$ on plants of Colorado (Rollins 1941a) shows that an unusual chromosome-number pattern is geographically widely dispersed within *A. holboellii* as a whole. This species is part of, and more or less at the center of, an agamic complex of species.

Arabis inyoensis is a taxonomic puzzle mainly because no two collections seem to match even in the most obvious details. We have attempted to see if the various specimens we have referred to *A. inyoensis* could be accounted for by hybridization between different taxa of *Arabis* in the area where it occurs. However, it has not been possible to assign putative parental taxa that would satisfactorily explain the specimens placed together under the name *A. inyoensis*. We recognize that the populations represented by our specimens are somewhat variable and that these have some features in common with *A. pulchra* var. *munciensis*.

Arabis inyoensis was shown to be self-compatible by isolating individual plants and mechanically self-pollinating specific flowers. When this procedure was followed, a good seed-set resulted. In isolated plants, emasculated flowers with no chance for pollination still produced a limited seed-set. From 96 ovules, seven viable seeds arose. Thus, approximately 7.3 per cent of the ovules matured into seeds without fertilization or even pseudogamy. This is strong evidence that apomixis is operative in *A. inyoensis*.

The chromosome number of $2n = 21$ in *Arabis pulchra* var. *munciensis* and in var. *gracilis* and of $2n = 21$ and $2n = 23$ in *A. inyoensis*, strongly suggests the possibility of another complex of apomicts in the group of species associated with *A. pulchra*. In Plate I, fig. 1, trivalent and tetravalent chromosome associations, as well as univalents, are clearly shown. If these data were to be coupled with definite evidence of interspecific hybridization, an adequate basis for explaining the peculiar variability to be seen among the specimens would surely be established. *Arabis pulchra* var. *pulchra* is a stable taxonomic entity when compared with var. *gracilis* and var. *munciensis*, the latter being quite variable. On the basis of our present knowledge of the species, we would predict that var. *pulchra* with its chromosome complement of $2n = 14$ is sexual and that var. *gracilis* and var. *munciensis* are largely apomictic.

Cakile

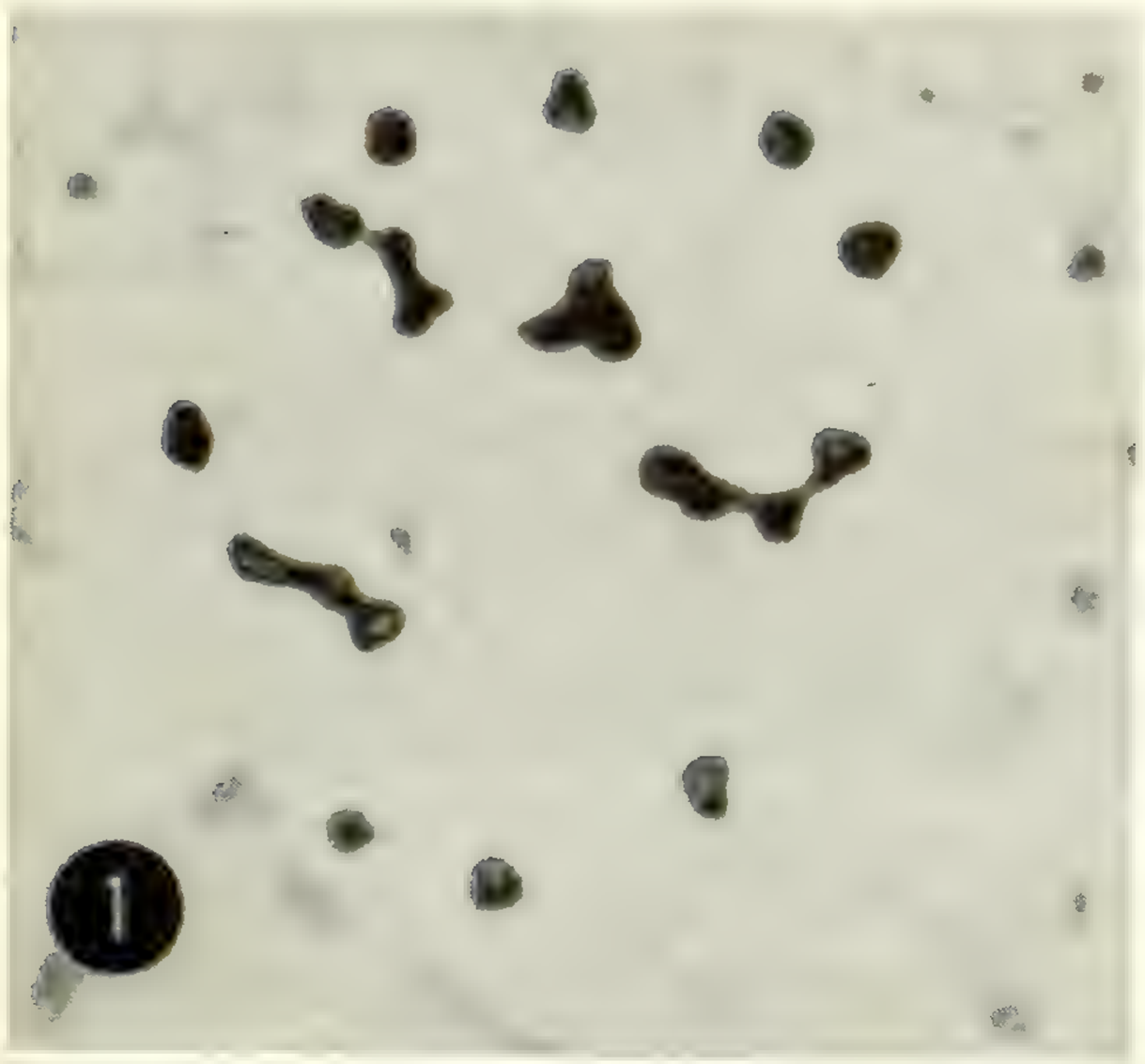
Three collections of seeds of *Cakile*, one from Duval Co., Florida, one from Monroe Co., Florida and one from St. John Beach, Trunk Bay, Virgin Islands, have been supplied to us by Dr. C. E. Wood, Jr. Plants from these have been grown and a chromosome count on each proved to be $2n = 18$. This material was turned over to Mr. James E. Rodman who has now undertaken a major study of the genus *Cakile* as it occurs in the Western Hemisphere. He will report on the identity of the material referred to and more fully on the cytology at a later date.

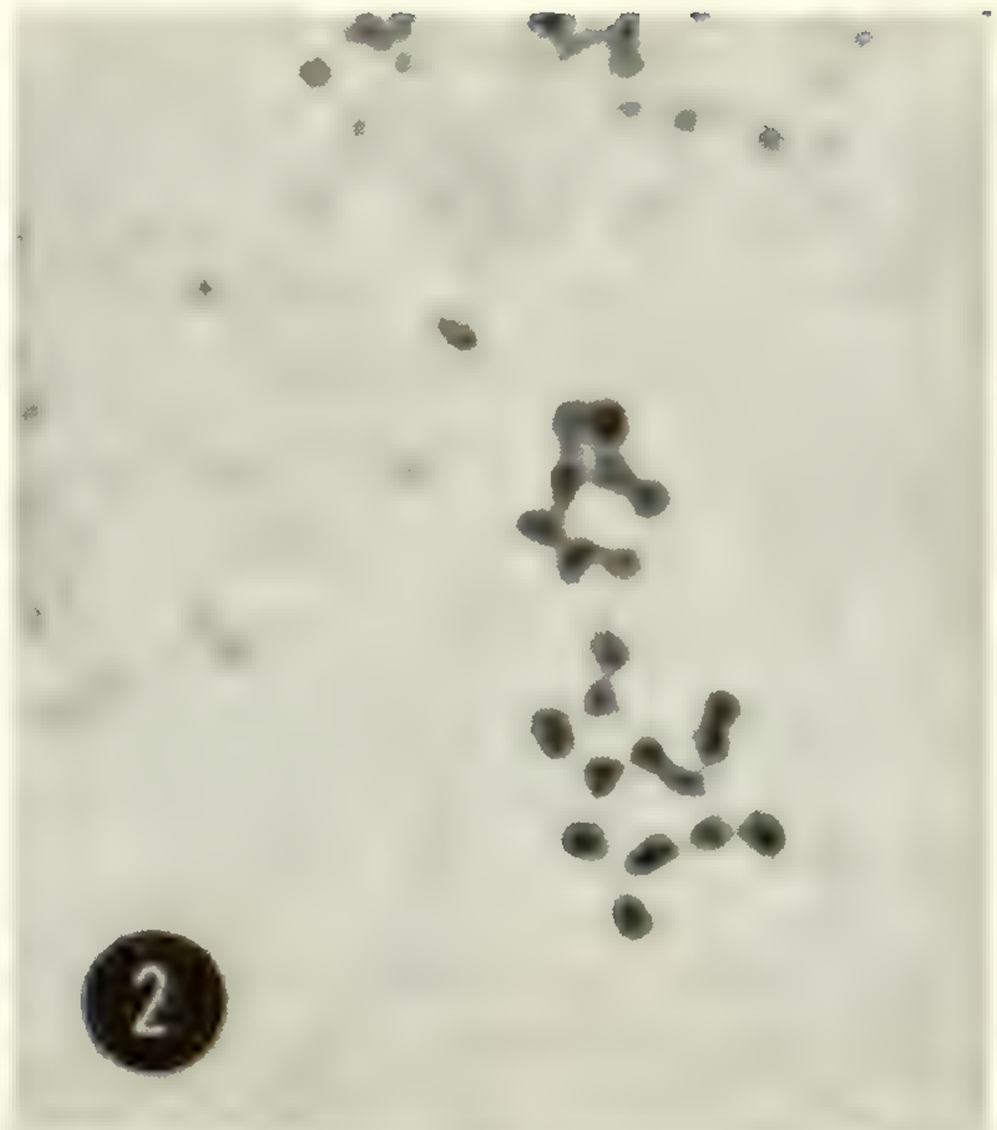
Caulanthus

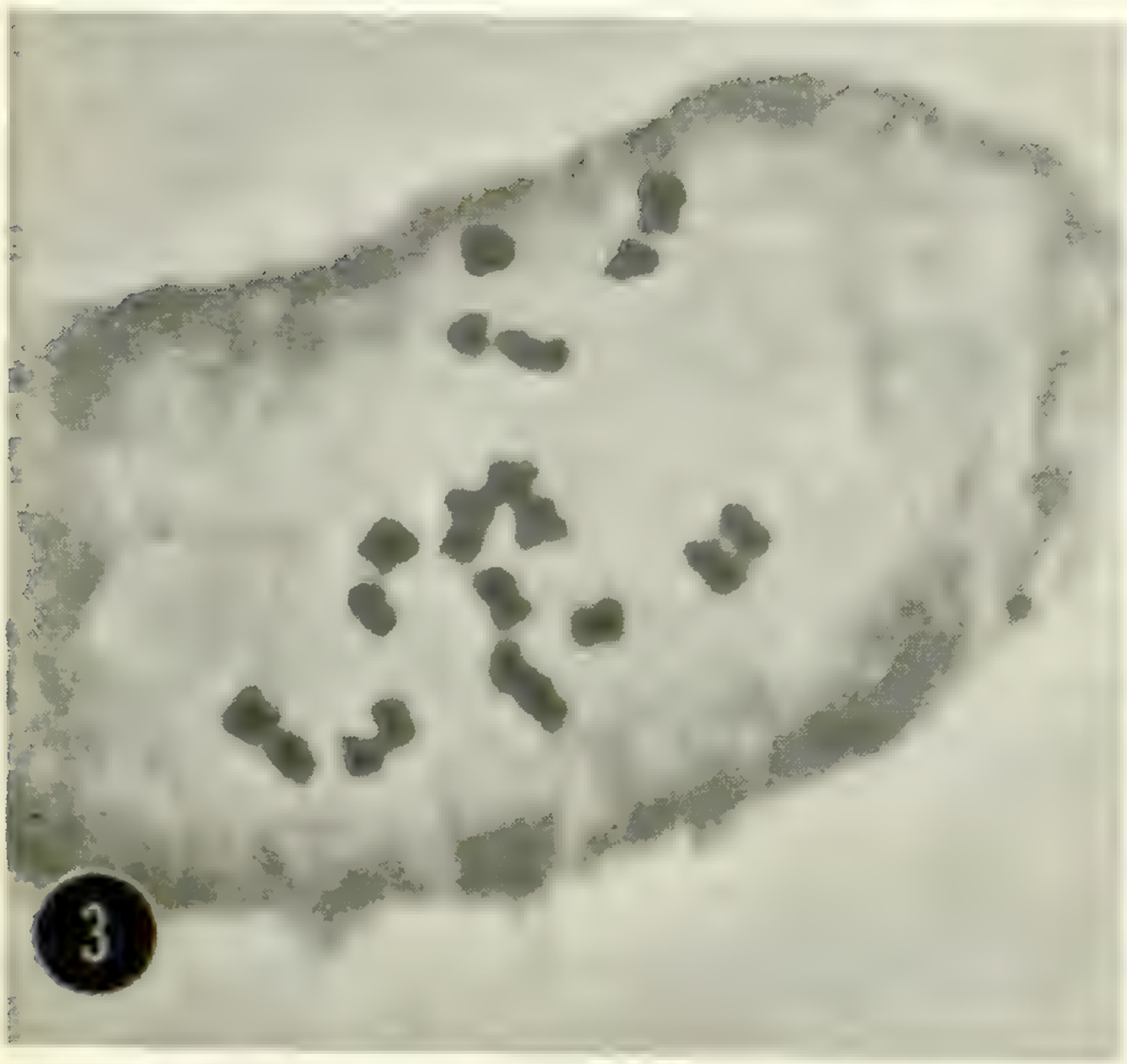
C. cooperi (Wats.) Payson

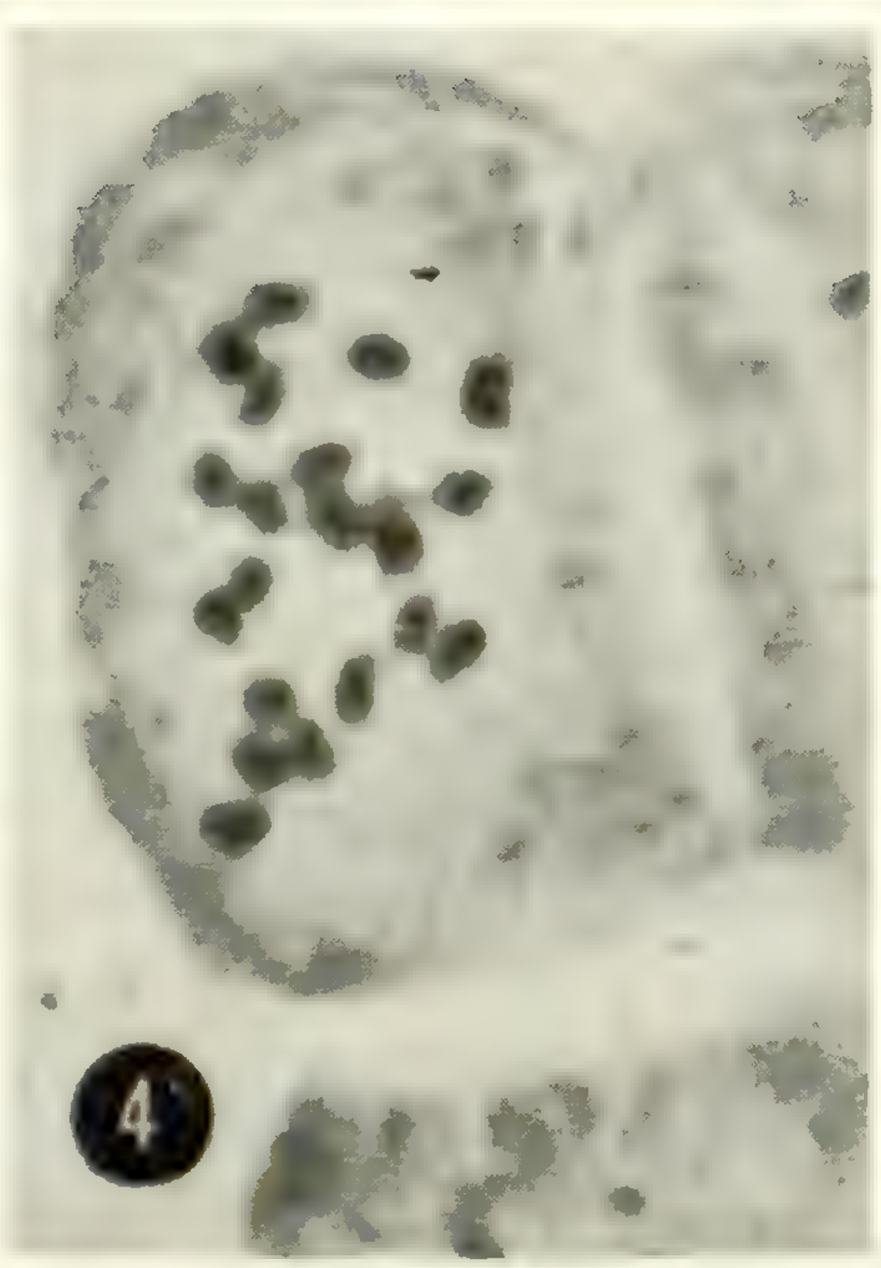
$n = 14$: Inyo Co., California, Rollins 6715; 6737; 6752.

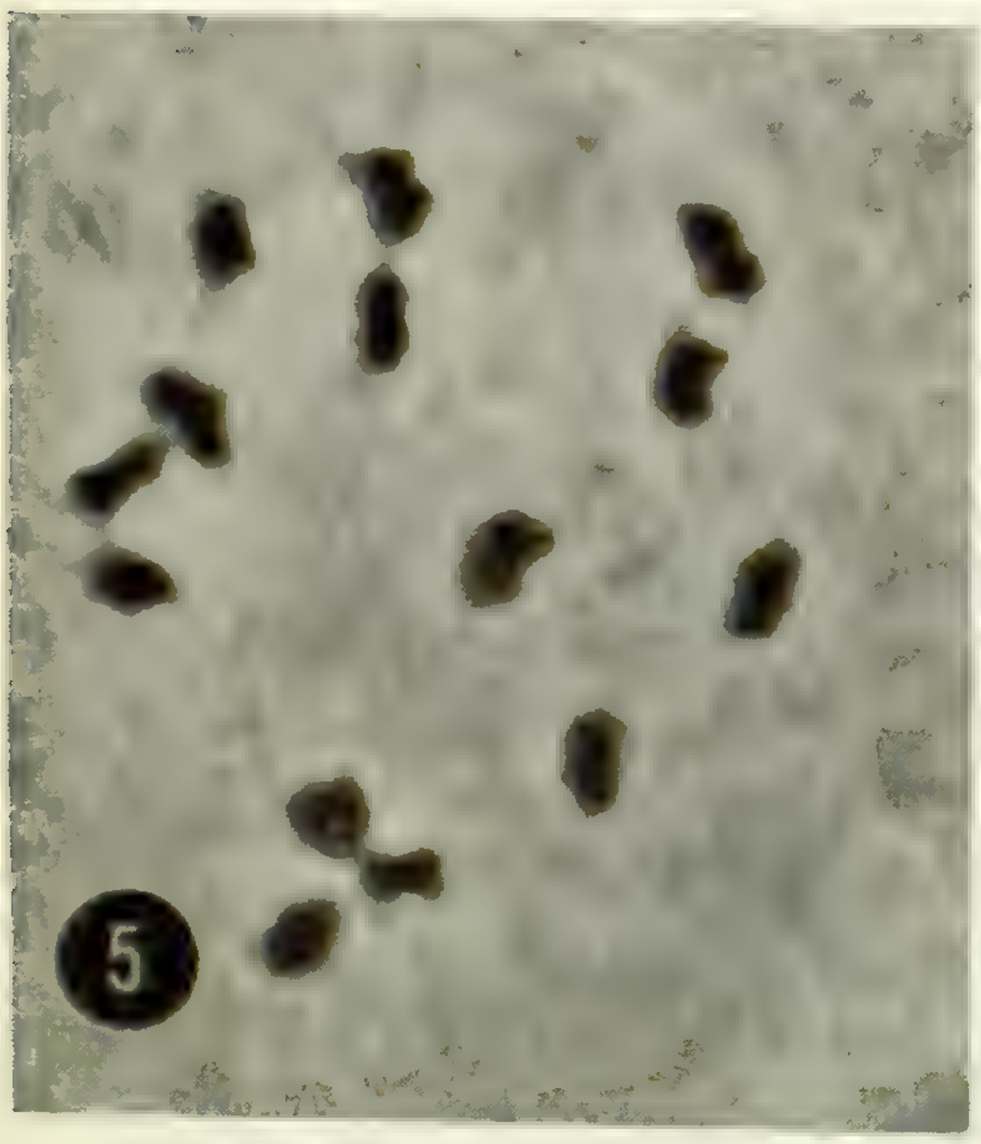
$n = 14$: Kern Co., California, Rollins 6726, Plate I, fig. 5.











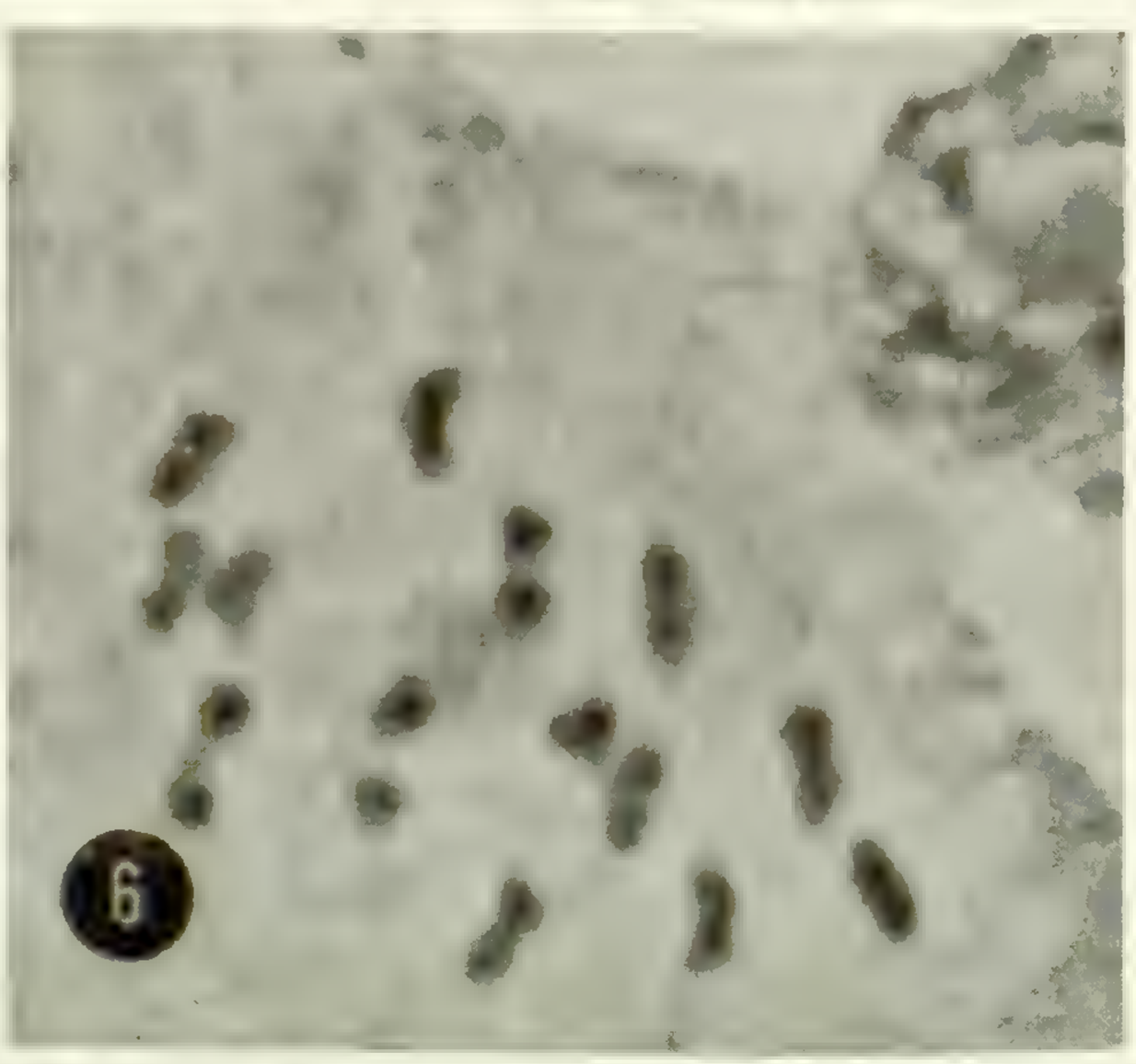


PLATE I. FIG. 1, PMC, diak., *Arabis inyoensis,* Reveal & Beatley 1475. FIG. 2, root-tip cell, *Arabis pulchra* var. *munciensis,* Beatley & Bostick 4048. FIG. 3, root-tip cell, *Arabis sparsiflora* var. *subvillosa,* Al-Shehbaz 6950. FIG. 4, same as fig. 2. FIG. 5, PMC, half of A_I, *Caulanthus cooperi,* Rollins 6726. FIG. 6, PMC, diak., *Caulanthus inflatus,* Rollins 6731. All figures × ca. 2650.

C. coulteri Watson
$n = 14$: Kern Co., California, Rollins 6724, Plate II, fig. 8.
C. glaucus Watson
$n = 10$: Inyo Co., California, Rollins 6736, Plate II, fig. 7.
C. inflatus Watson
$n = 14$: San Bernardino Co., California, Rollins 6731, Plate I, fig. 6; Rollins 6754.
C. inflatus (?)
$n = 14$, $2n = 28$: plants from seeds of Al-Shehbaz 6945. San Bernardino Co., California.
C. lasiophyllus (H. & A.) Payson var. *lasiophyllus*
$n = 14$: Inyo Co., California, Rollins 6714.
$n = 14$: Kern Co., California, Rollins 6722.
$n = 14$: San Bernardino Co., California, Rollins 6732.
$n = 14$: plants from seeds of Al-Shehbaz 6948, San Bernardino Co., California.

Four different populations of *Caulanthus cooperi* were sampled by fixing buds in the field. Some irregularities and some stickiness was seen, but a consistent chromosome number of $n = 14$ was found in all populations. This number is in line with that of most other species of *Caulanthus* and adds some evidence which favors the inclusion of the species in this genus. The flowers of *C. cooperi* are "streptanthoid" which also suggests that Payson was correct in placing it in *Caulanthus*. The finding of $n = 10$ in *C. glaucus* was a surprise because we had come to expect $n = 14$ in the uncounted species of the genus. To be sure, we had earlier reported $n = 10$ for *C. inflatus*, but our most recent counts, which have been double-checked, show the count for *C. inflatus* to be $n = 14$. A collection, *Al-Shehbaz 6945*, has been tentatively referred to *C. inflatus*. The greenhouse-grown plants differ from specimens of wild populations in a number of significant ways and the material may represent a different taxon. There is no doubt about it being *Caulanthus*, but whether the material should be called *C. inflatus* is somewhat open to question. A specimen has been placed in the Gray Herbarium for further reference.

Cardamine

C. flaccida Chamisso & Schlechtendahl
$n = 8$: plants from seeds of Meyer 9589, Mas Atierra, Juan Fernandez Islands, Chile.

As currently interpreted, *Cardamine flaccida* is a highly variable species with a geographic range that extends through much of the Cordilleran region of South America, and northward into Mexico. It is doubtful whether all variants now placed in this species are in reality a single taxon of specific rank. For this reason, the identity of the material studied is somewhat open to question and may need to be changed once the taxonomy of *C. flaccida* and its near relatives has been fully worked out. The chromosome number fits with that of a number of North American species

as reported by Mulligan (1965) as well as many species from elsewhere (Manton 1932).

Descurainia

D. pinnata (Walt.) Britton subsp. *halictorum* (Cockerell) Detling
$n = 7$, $2n = 14$: plants from seeds of Moran 12500, La Bocana, Baja California, Mexico.

Greenhouse-grown plants of this taxon proved to be not only self-compatible but strongly autogamous as well. With insects excluded and without any manipulation whatever, a full set of fruits and seeds were produced.

Draba

D. asprella Green
$n = 16\pm$: Coconino Co., Arizona, Rollins 6766.

D. brachycarpa Nuttall
$2n = 24$: plants from seeds of D. S. & H. B. Correll 36897, Kaufman Co., Texas.

D. corrugata Watson var. *demareei* (Wiggins) C. L. Hitchcock
$n = 12$: plants from seeds of Moran 15267, San Pedro Martir Cerro, Baja California, Mexico. Plate III, fig. 12.

D. cuneifolia Nuttall
$n = 16$: plants from seeds of D. S. & H. B. Correll 30840, Pecos Co., Texas.

D. platycarpa Torrey & Gray
$n = 16$, $2n = 32$: plants from seeds of D. S. & H. B. Correll 30763, Kinney Co., Texas.

The morphological distinctions between *Draba cuneifolia* and *D. platycarpa* are sharp and consistent. However, *D. platycarpa* has often been treated as a variety of *D. cuneifolia*. For this reason, having material of both taxa available for study, we looked at the chromosomes and chromosome number with special interest. The number and general size relationships of the chromosomes of both species are similar. Nothing definitive either supporting the presently accepted taxonomy or suggesting the recognition of two infraspecific taxa could be seen in the chromosomes.

Dithyrea

D. californica Harvey
$n = 10$: San Bernardino Co., California, Rollins 6702; 6703, Plate III, fig. 13 & 14.

D. wislizenii Engelmann
$n = 9$: Coconino Co., Arizona, Rollins 6777; Washington Co., Utah, Rollins 6789, Plate II, fig. 9.
$2n = 18$: Navajo Co., Arizona, Rollins 67115, Plate II, fig. 11.

The above chromosome numbers are the same as those previously

reported (Rollins 1966) and serve to confirm that the aneuploid relationship between *Dithyrea californica* and *D. wislizenii* is consistent taking different populations and a broadened geographic area into account. In the three populations of *D. wislizenii* sampled, all plants possessed densely pubescent siliques. However, in one population 38 miles east of Kanab, Kane Co., Utah (*Rollins 6784*) not fixed for cytological sampling, an examination of 100 plants at random showed 47 plants with glabrous fruits and 53 plants with pubescent fruits. This approximate 1:1 ratio of glabrous- to pubescent-fruited plants is different from the population previously analyzed (Rollins 1958) which was roughly 1:3 glabrous to pubescent. The experimental data from crosses involving glabrous- and pubescent-fruited plants showed that a 1:1 ratio resulted when heterozygous glabrous-fruited individuals were crossed with homozygous pubescent-fruited individuals. That wild populations with this same ratio of glabrous to pubescent fruits existed could have been confidently predicted, but this is the first confirmation that such populations are, in fact, to be found in nature.

The chromosomes of the somatic cell of *Dithyrea wislizenii* shown in Plate II, fig. 11, were stained with both Feulgen and acetocarmine which produced a more intensely refractive photographic image than is usual. The difference in size between A_I and M_I chromosomes is ordinarily great. However, in *D. californica,* the difference is unusually large as is shown in Plate III, fig. 13 and 14.

Dryopetalon

D. runcinatum Gray var. *laxiflorum* Rollins

$n = 12$: plants from seeds of D. E. Breedlove 15892, Municipio Mocorito, Sinaloa, Mexico, Plate II, fig. 10.

This is the first chromosome number report for *Dryopetalon* which is a relatively small genus of southwestern United States and northwestern Mexico (Rollins 1941b). Flowers of living plants show the white petals to be oriented in a paired upper and lower position and with the anthers of all stamens introrse. The stigma is definitely bilobed.

Erysimum

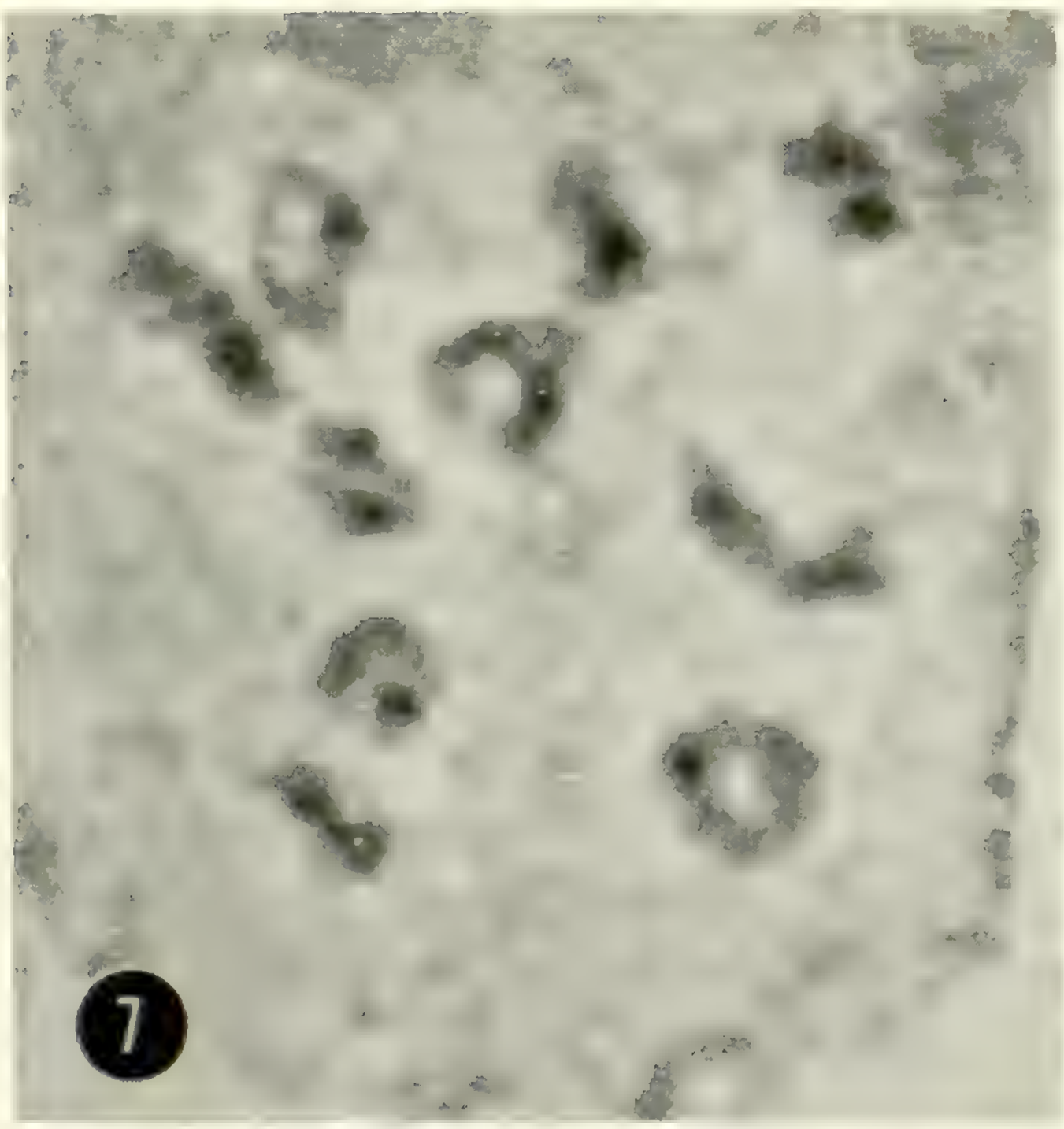
E. moranii Rollins

$2n = 36$: plants from seeds of Moran 15116, Guadalupe Island, Baja California, Mexico.

E. suffrutescens (Abrams) Rossbach var. *lompocense* Rossbach

$n = 18$: San Luis Obispo, California, Rollins 6727.

The plants grown from *Moran 15116,* the type number of the species, are subshrubby and very much branched. The species was only recently described (Rollins 1970). The chromosome complement in *Erysimum moranii* is unusual in that the chromosomes differ greatly in size. The



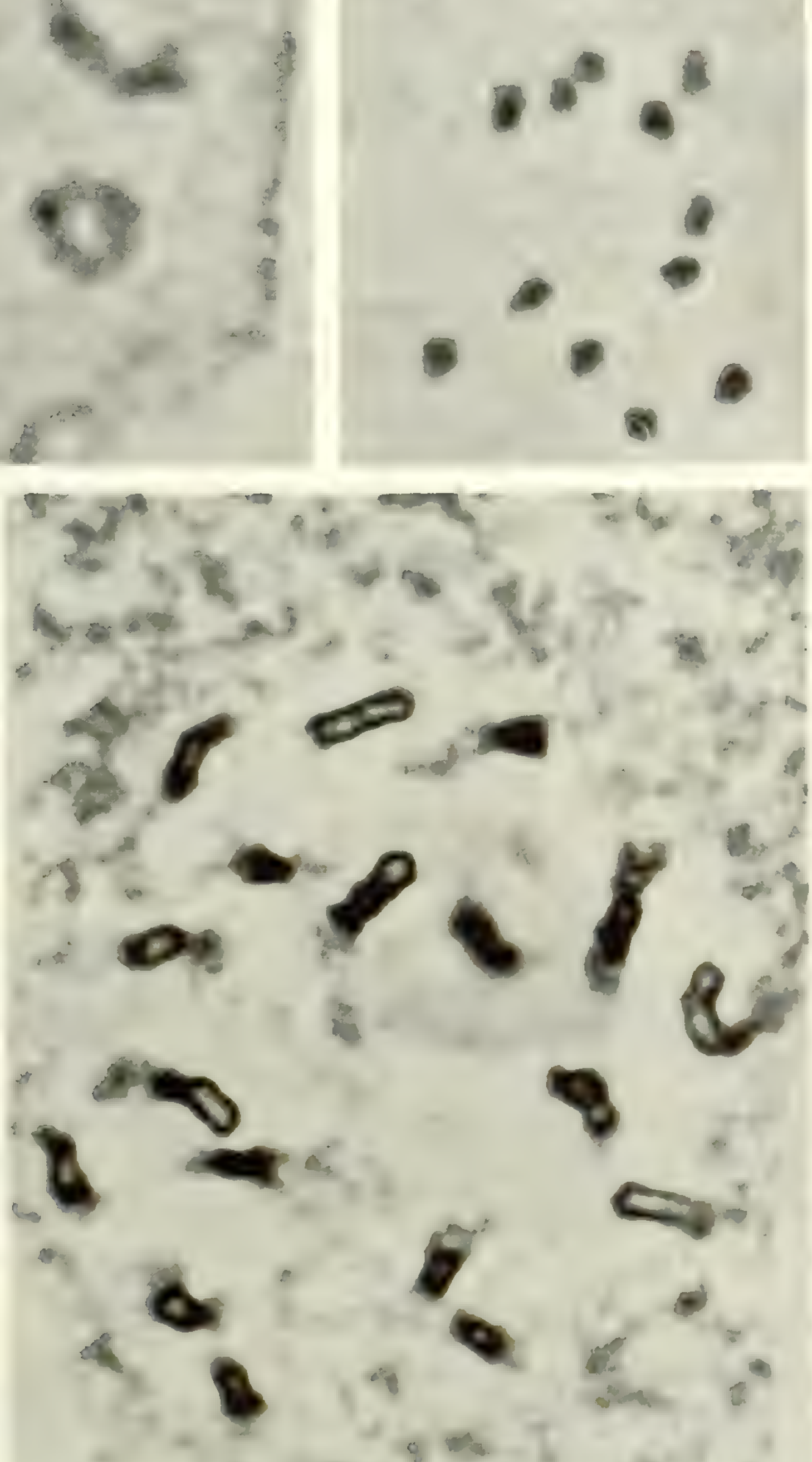
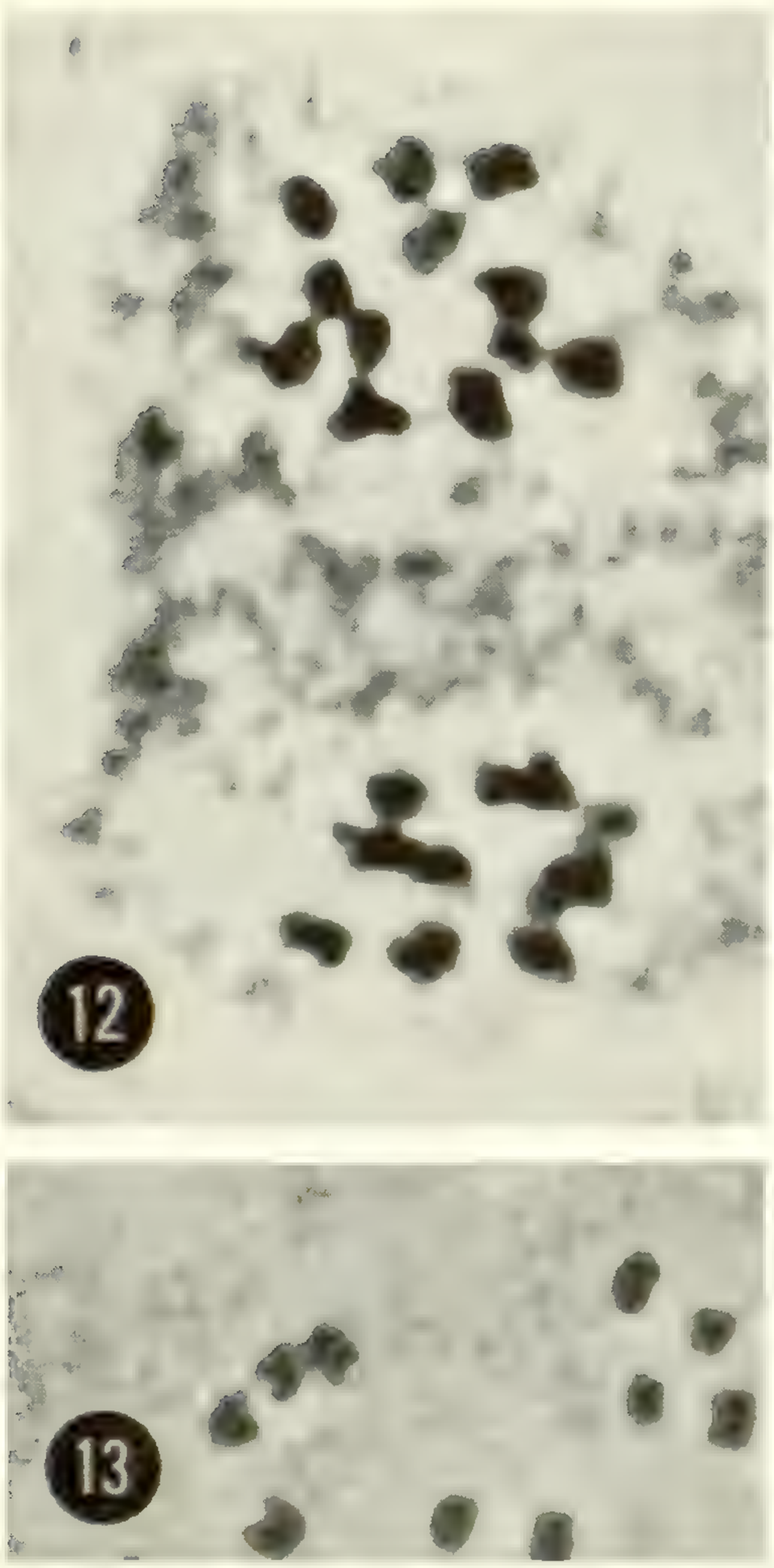


PLATE II. FIG. 7, PMC, diak., *Caulanthus glaucus,* Rollins 6736. FIG. 8, PMC, half of A_I, *Caulanthus coulteri,* Rollins 6724. FIG. 9, PMC, half of A_I, *Dithyrea wislizenii,* Rollins 6789. FIG. 10, PMC, M_I, *Dryopetalon runcinatum* var. *laxiflorum,* Breedlove 15892. FIG. 11, tapetal cell, *Dithyrea wislizenii,* Rollins 67115. All figures × ca. 2650.



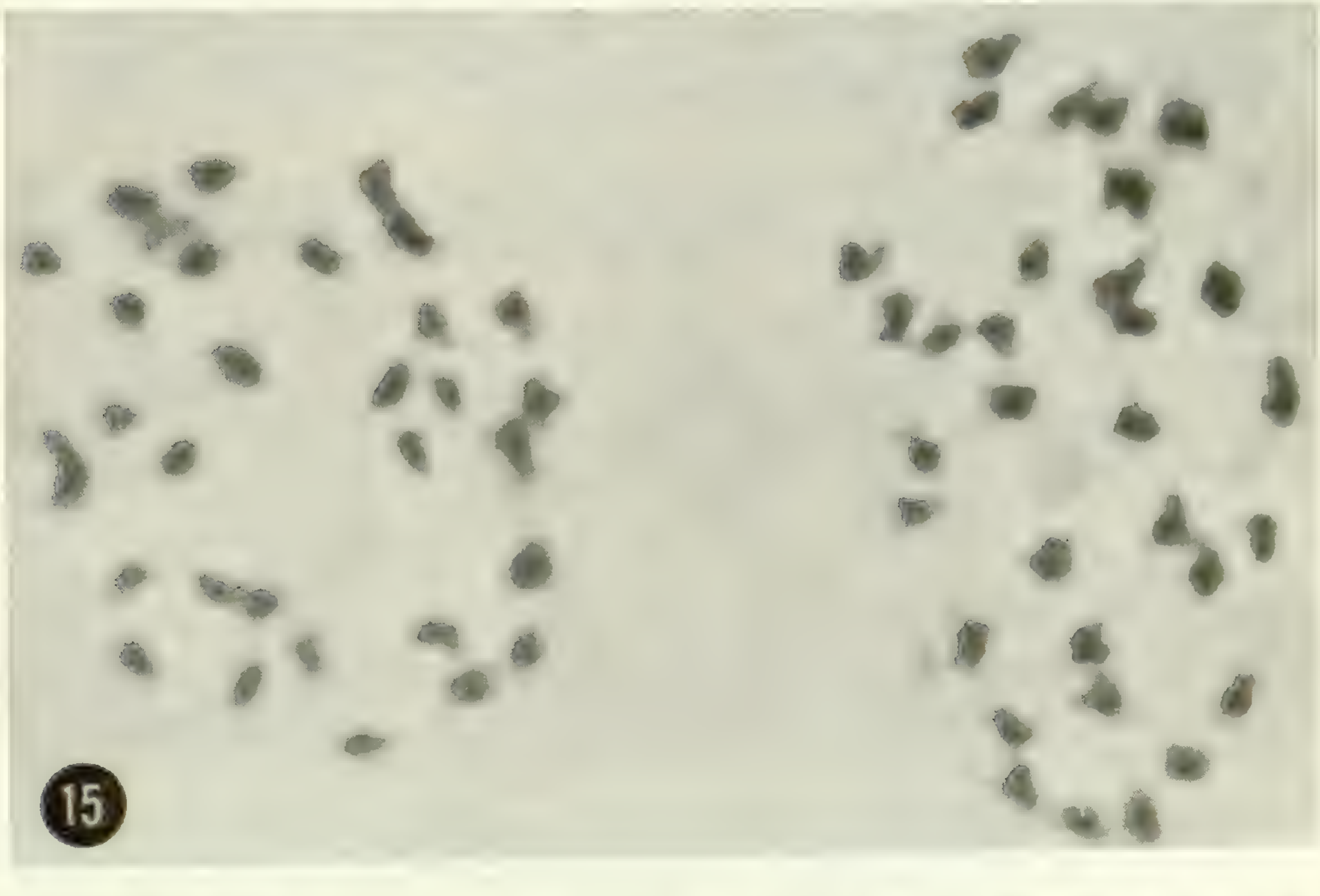


PLATE III. FIG. 12, PMC, A_I, *Draba corrugata* var. *demareei,* Moran 15267. FIG. 13, PMC, half of A_I, *Dithyrea californica,* Rollins 6702. FIG. 14, PMC, M_I, *Dithyrea californica,* Rollins 6703. FIG. 15. PMC, late A_I, *Lepidium fremontii,* Rollins 6707. All figures × ca. 2650.

longest chromosome is nearly four times longer than the shortest chromosome, and there are many different sizes in between.

Lepidium

L. flavum Torrey
$n = 16$: Inyo Co., California. Rollins 6713.
L. fremontii Watson
$n = 32$: Clark Co., Nevada, Rollins 6707, Plate III, fig. 15; Inyo Co., California, Rollins 6717.
L. lasiocarpum Nuttall
$n = 16$: Clark Co., Nevada, Rollins 6706.
L. montanum Nuttall var. *canescens* (Thellung) C. L. Hitchcock
$2n = 32$: plants from seeds of Beatley 5998, Nye Co., Nevada.
L. montanum Nuttall var. *jonesii* (Rydberg) C. L. Hitchcock
$n = 32$: Coconino Co., Arizona, Rollins 6781.
L. virginicum L.
$2n = 32$: plants from seeds of Thieret 29936, Morehouse Parish, Louisiana.

The two high polyploids ($n = 32$), *Lepidium fremontii* and *L. montanum* var. *jonesii* are perennial and either shrubby as in the former or subshrubby as in the latter. Except for *L. montanum* var. *canescens*, the other taxa reported upon above are herbaceous annuals. From the data so far available (c.f., Manton 1932; Mulligan 1961; Rollins 1966), it appears that most of the herbaceous species of *Lepidium* in North America are either diploid or tetraploid based on x = 8. A notable exception is *L. ramosissimum* Nels. with $2n = 64$ (Mulligan 1961).

Lesquerella

L. arizonica Watson
$n = 5$, $2n = 10$: Coconino Co., Arizona, Rollins 6762, Plate IV, fig. 19.
$2n = 10$: Coconino Co., Arizona, Rollins 6776.
$n = 10$: Coconino Co., Arizona, Rollins 67100.
L. auriculata (Engelmann & Gray) Watson
$n = 8$, $2n = 16$: plants from seeds of Barclay 3058. Garfield Co., Oklahoma.
L. cinerea Watson
$n = 5$: Yavapai Co., Arizona, Rollins 67109, Plate IV, fig. 18; same county, Rollins 67110; Coconino Co., Arizona, Rollins 6770–probably $2n = 10$.
L. douglasii Watson
$n = 5$, $2n = 10$: Lincoln Co., Washington, Rollins & M. Ownbey 6794.
L. fendleri (Gray) Watson
$n = 6$: McKinley Co., New Mexico, Rollins 67116.
$2n = 12$: Sandoval Co., New Mexico, Rollins 67122; plants from seeds of Rollins & Correll 6616, Kinney Co., Texas.

L. gordonii (Gray) Watson
$n = 6$, $2n = 12$: Mohave Co., Arizona, Rollins 6760.
L. intermedia (Watson) Heller
$n = 18$: Mohave Co., Arizona, Rollins 6797.
L. lindheimeri (Gray) Watson
$n = 6$: near Matamoras Airport, Tamaulipas, Mexico, Rollins 6701, Plate IV, fig. 16.
L. peninsularis Wiggins
$n = 24\pm$: Sierra San Pedro Martir, Baja California, Mexico, Moran & Thorne 14379.
L. pinetorum Wooton & Standley
$n = 5$: Yavapai Co., Arizona, Rollins 67107. Plate IV, fig. 21.
$2n = 10$: Bernanillo Co., New Mexico, Rollins 67119. Plate IV, fig. 20.
L. rectipes Wooton & Standley
$n = 9$, $2n = 18$: plants from seeds of Gentry & Davidse 1794, San Juan Co., Utah, Plate IV, fig. 17.
$n = 20\pm$, uncertain count: McKinley Co., New Mexico, Rollins 67117.
L. tenella Nelson
$2n = 10$: Riverside Co., California, Rollins 6755.

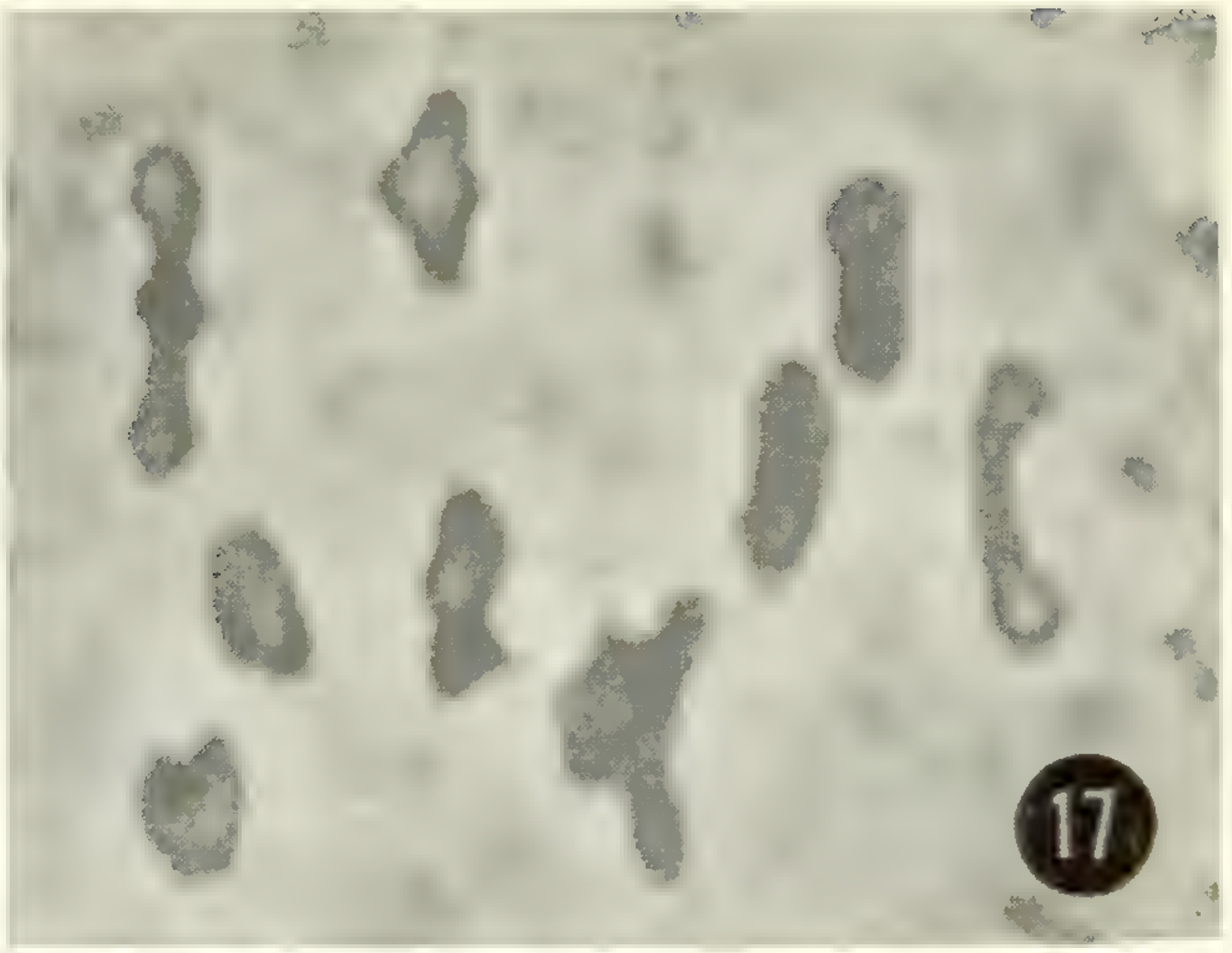
In a previous report on chromosome numbers in *Lesquerella* (Rollins 1966) polyploid populations were mentioned based on numbers of $x = 6$ and $x = 9$. It is now clear that polyploidy occurs within *L. arizonica* which has a fundamental number of $x = 5$. The diploid, *Rollins 6762*, was collected within 20 miles of the tetraploid, *Rollins 67100*. Both populations were in an open piñon-juniper woods where limestone chip is prevalent. The previous report of $2n = 18$ for *L. intermedia* and the present one of $n = 18$ also shows that polyploidy occurs in this species. It is probable that both of these records represent polyploidy based on the fundamental number $x = 6$ because the species most closely related to *L. intermedia* have $n = 6$.

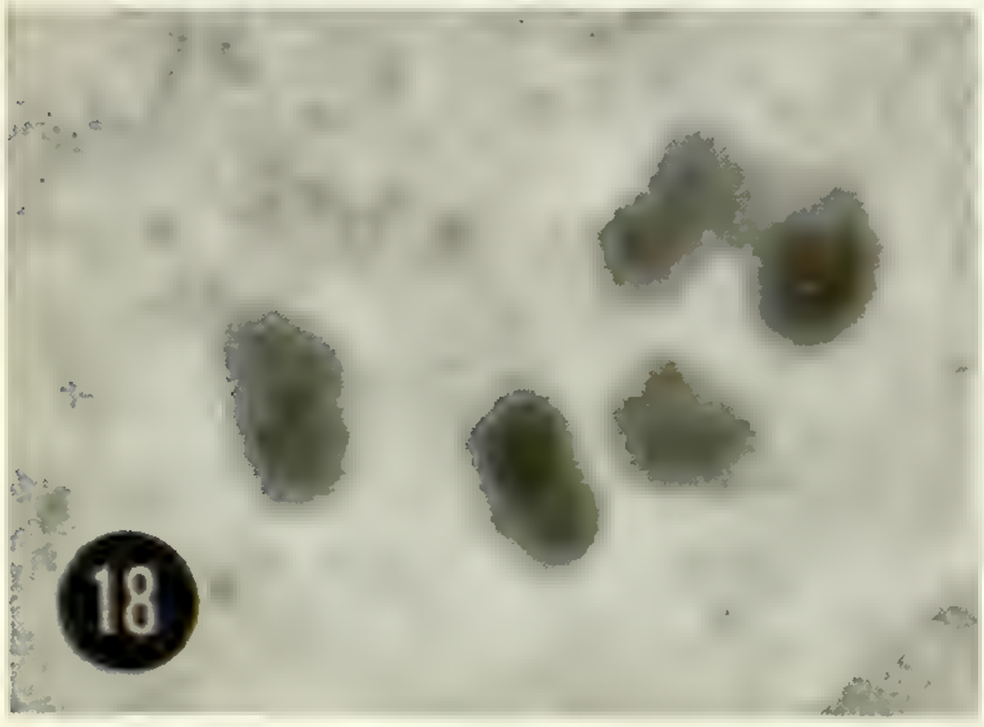
We are somewhat uncertain as to the number $n = 24$ for *Lesquerella peninsularis* because all figures showed some clumping of the chromosomes. However, we can be certain that the species is a polyploid. The evidence also shows that *L. rectipes* has polyploid populations even though we were not able to obtain a certain count on the New Mexico population cited.

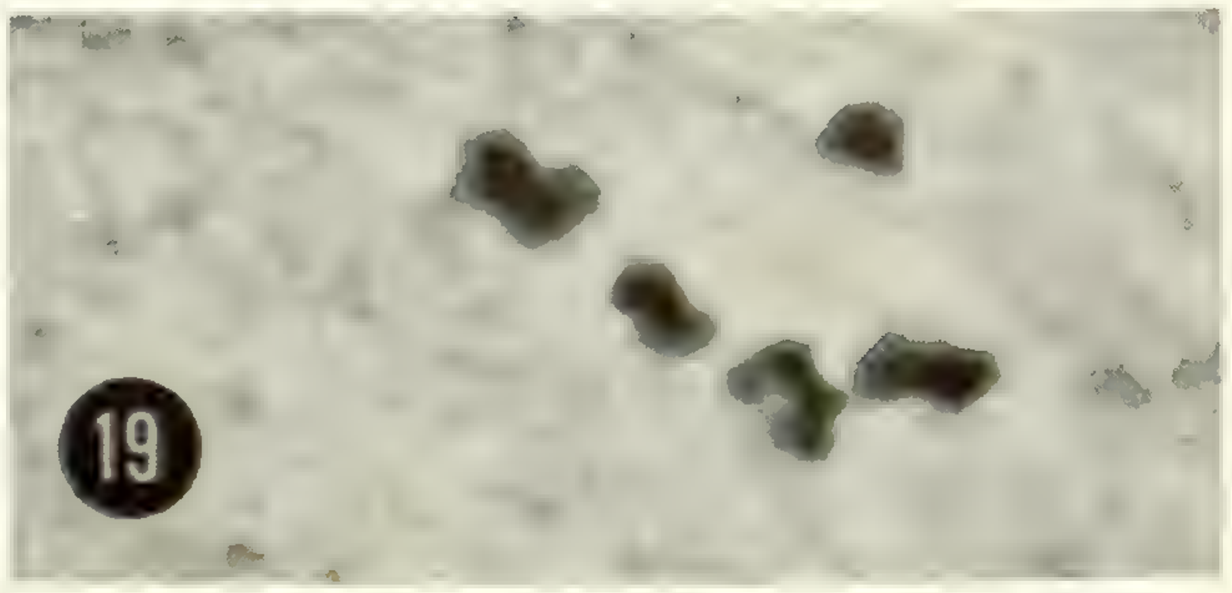
The above citation is the first record of *Lesquerella lindheimeri* from Mexico. However, this species is characteristic of the coastal plain of extreme southern Texas and was to be expected from adjacent Mexico. The chromosome number $n = 6$ conforms to the number present in the Texas populations cited in an earlier paper (Rollins *loc. cit.*).

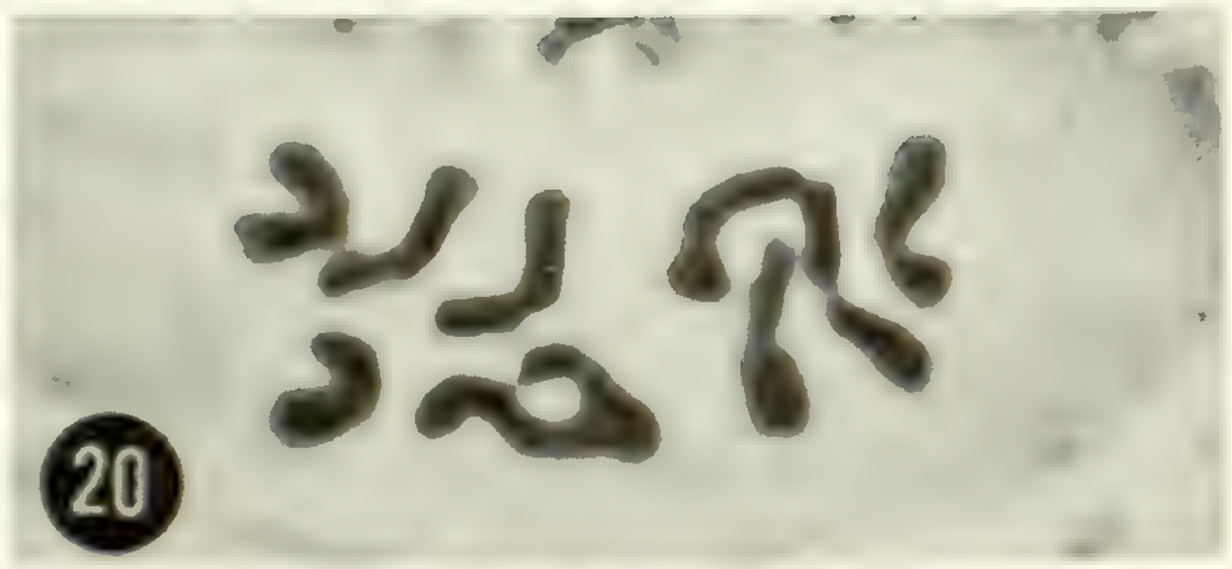
Ornithocarpa

O. torulosa Rollins
$n = 24$, $2n = 48$: plants from seeds of Breedlove 15888, Durango, Mexico.









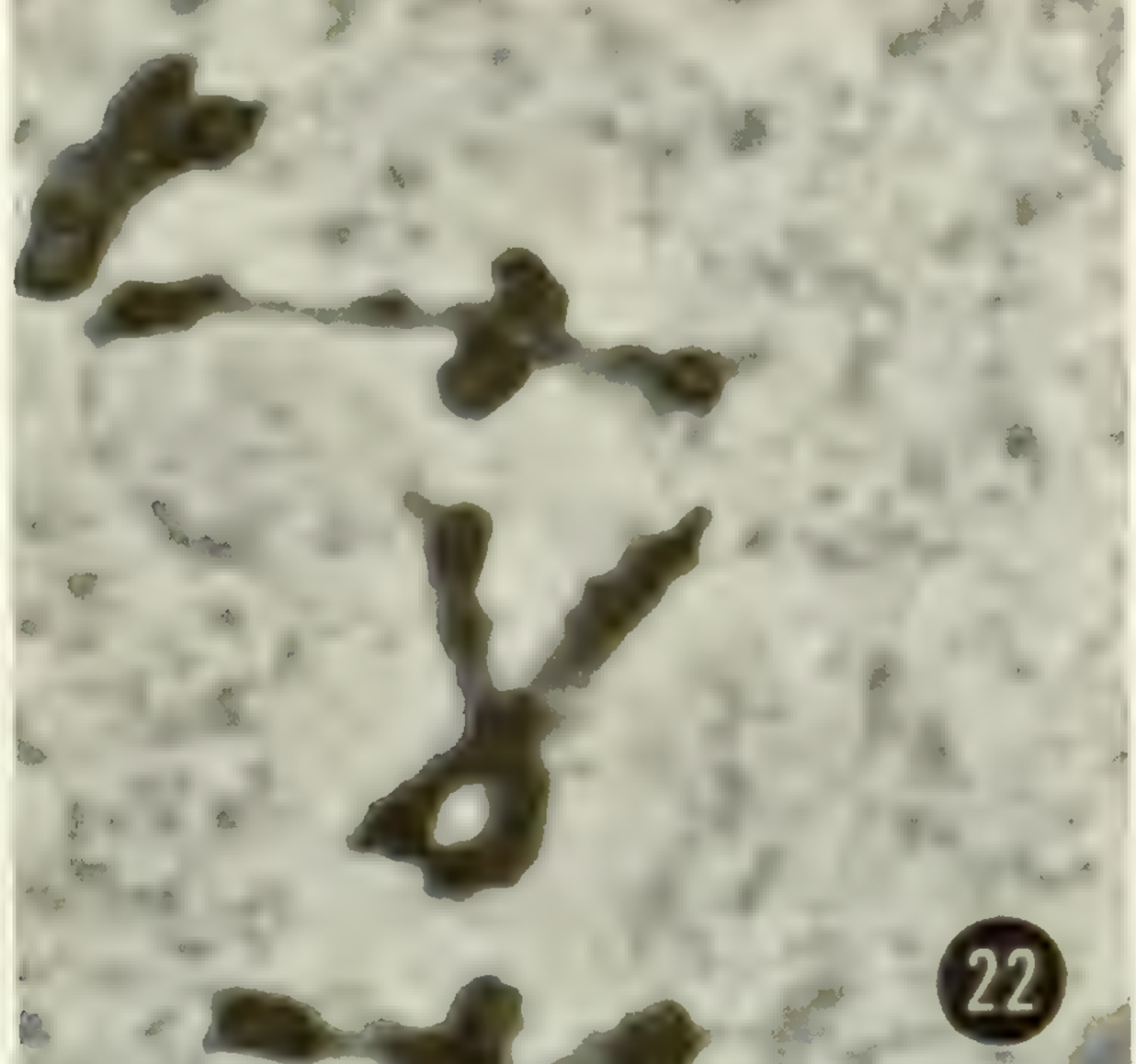
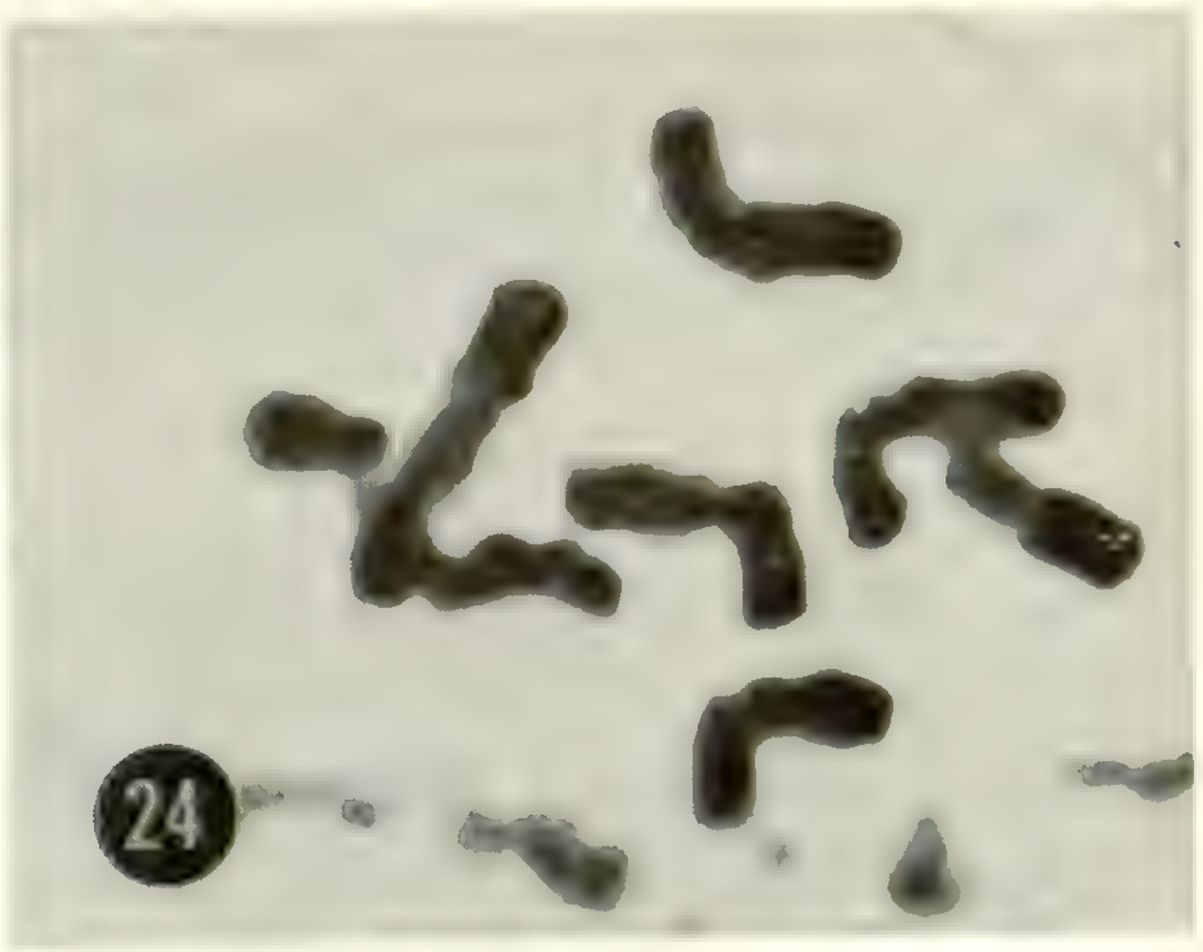


PLATE IV. FIG. 16, PMC, A_I, *Lesquerella lindheimeri,* Rollins 6701. FIG. 17. PMC, M_I, *Lesquerella rectipes,* Gentry & Davidse 1794. FIG. 18, young pollen grain, 1st div. *Lesquerella cinerea,* Rollins 67109. FIG.19, PMC, half of A_I, *Lesquerella arizonica,* Rollins 6762. FIG. 20, somatic anther cell, *Lesquerella pinetorum,* Rollins 67119. FIG. 21, PMC, A_I, *Lesquerella pinetorum,* Rollins 67107. FIG. 22, PMC, diak.–M_I, *Physaria geyeri,* Ownbey 3467. All figures × ca. 2650.



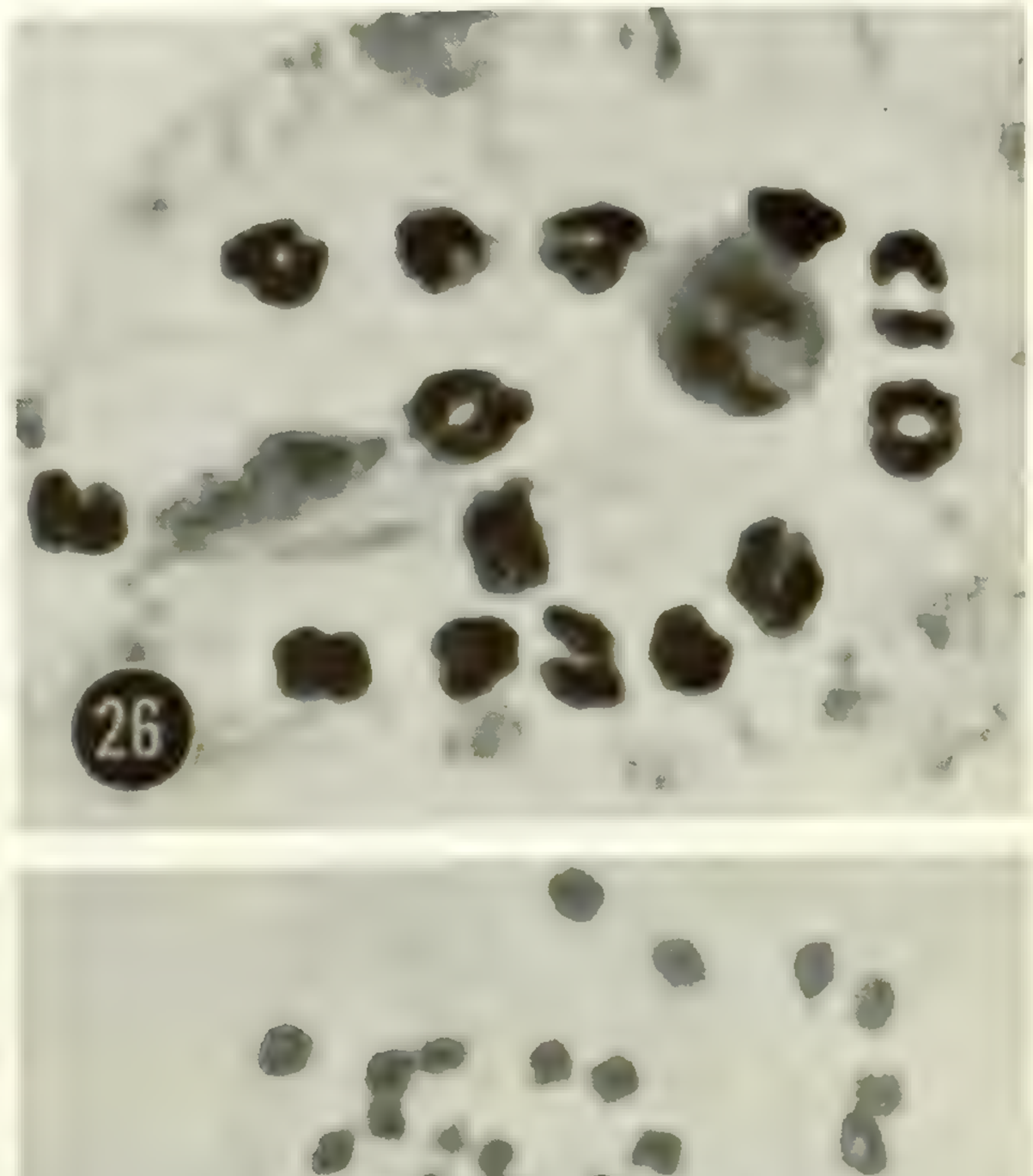


PLATE V. FIG. 23, young pollen grain, *Physaria geyeri*, Ownbey 3467. FIG. 24, young pollen grain or possibly PMC, *Physaria chambersii*, Rollins 6788. FIG. 25, PMC, A_I, *Sisymbrium amphibiguum*, Rollins 67101. FIG. 26, PMC, diak., *Sibara angelorum*, Moran 12345. FIG. 27, root-tip cell, *Pringlea antiscorbutica*, Montreal Bot. Gard. FIG. 28, root-tip cell, *Stanleya pinnata* subsp. *inyoensis*, Beatley 9010. All figures × ca. 2650.

Since publishing this species as new (Rollins 1969) and giving the somatic chromosome number of $2n = 48$, we have examined the meiotic chromosomes and additional root-tip material both of which confirm the original chromosome number determination.

Physaria

P. chambersii Rollins

$n = 8$: Washington Co., Utah, Rollins 6788, Plate V, fig. 24.

P. geyeri (Hook.) Gray

$n = 4$: Spokane Co., Washington, M. Ownbey 3467, Plate IV, fig. 22 and Plate V, fig. 23.

The above tetraploid count for *P. chambersii* was to be expected on the basis of the data of Mulligan (1968) in which he showed that races with $2n = 16$ predominate in southern Utah. Also, the count for *P. geyeri* is the expected number. Mulligan (*loc. cit.*) has transferred *P. geyeri* to the genus *Lesquerella* but we do not agree with this disposition of the species. The chromosomes of *P. geyeri* are much more like those of other species of *Physaria* than of any of the species of *Lesquerella* we have studied. This is clearly shown by comparing Plate V, fig. 23, showing the chromosomes of an immature pollen grain of *Physaria* with those of *Lesquerella cinerea,* Plate IV, fig. 18, also from an immature pollen grain. A full discussion of the issue will be presented in a forthcoming monograph of *Lesquerella* now in the late stages of preparation.

Pringlea

P. antiscorbutica R. Brown

$2n = 24$: plants from seeds received from the Montreal Botanical Garden.

The original seeds from which the plants at the Montreal Botanical Garden were derived presumably came from a French expedition to the Kerguelen Islands. We have grown plants of this species for several years in the greenhouse, but we have not been able to bring them into flower. Our chromosome count is the same as the previous count given by Hamel (1951).

Rorippa

R. nasturtium-aquaticum (L.) Hayek

$2n = 32$: plants from seeds of Rüdenberg s.n., Monterey Co., California.

According to Green (1962), the watercresses are all introductions from the Old World. They are found widely distributed in the Western Hemisphere and often appear to be native. His map of distributions shows only *R. nasturtium-aquaticum* in California, the central and southerly states, and central and South America. Our material is obviously of the diploid *R. nasturtium-aquaticum,* not *R. microphyllum* which has $2n = 64$ and has a more northerly distribution in North America.

Selenia

S. dissecta Torrey & Gray

$n = 7$: Brewster Co., Texas, Rollins & Correll 6633.

S. grandis Martin

$n = 12$: plants from seeds of Correll 36755, Hidalgo Co., Texas.

Three species of Selenia have now been counted and no two appear to have the same chromosome number. The count of $n = 12$ for *S. grandis* reaffirms previous results on plants from Dimmit Co., Texas (Rollins 1966). Arkansas material of *S. aurea* had $n = 23$. *Selenia dissecta* is very different morphologically from either one of these species. It is found only in New Mexico, extreme western Texas and adjacent Mexico.

Sibara

S. deserti (Jones) Rollins

$n = 14 \pm$: Inyo Co., California, Rollins 6746.

S. laxa (Watson) Greene

$n = 14$: Sierra San Borja, Baja California, Mexico, Moran 12318.

S. angelorum (Watson) Greene

$n = 14$: Bahia de los Angeles, Baja California, Mexico, Moran 12345. Plate V, fig. 26.

The previous chromosome count of $2n = 26$ for *Sibara deserti* (Rollins 1947) may be in error as judged by $2n = 28$ for most other species of the genus. However, our present material was not well enough fixed for us to be certain. The new counts of $n = 14$ for *S. laxa* and *S. angelorum* are the first for these species.

Sisymbrium

S. ambiguum (Watson) Payson

$n = 11$: Mohave Co., Arizona, Rollins 6796; Coconino Co., Arizona, Rollins 67101, Plate V, fig. 25.

S. linifolium Nuttall

$n = 7$: Kane Co., Utah, Rollins 6785.

S. salasugineum Pallas [Thellungiella salsuginea (Pall.) O. E. Schultz]

$2n = 14$: plants from seeds of Weber 12925, Park Co., Colorado.

We have followed Payson (1922) in the taxonomic placement of *Sisymbrium ambiguum*, but it is quite clear that this species should not be retained in *Sisymbrium*. The chromosome number of $n = 11$ supports this view and points to the possible association of *S. ambiguum* with *S. linearifolium* which also has a chromosome number of $n = 11$ (Rollins 1966). An extra B-chromosome may be readily seen in fig. 25 of Plate V. Although *S. salsugineum* fits the pattern for *Sisymbrium*, this species is often placed in the genus *Thellungiella*. Our count is the same as the two counts listed in Bolkovskikh *et al.* (1969).

Stanleya

S. elata Jones

$2n = 28$: Inyo Co., California, Rollins 6738. Plants from seeds of Al-Shehbaz 6944, Inyo Co., California.

S. pinnata (Pursh) Britton subsp. *pinnata*

$n = 14$: Kane Co., Utah, Rollins 6787.

S. pinnata subsp. *inyoensis* Munz & Roos

$n = 28$: Nye Co., Nevada, Rollins 6712; Inyo Co., California, Rollins 6747.

$2n = 56$: plants from seeds of Beatley 9010, Nye Co., Nevada, Plate V, fig. 28.

S. viridiflora Nuttall

$2n = 28$: plants from seeds of Al-Shehbaz 6938, Humboldt Co., Nevada.

In the arid valleys of eastern California and nearby Nevada, *Stanleya pinnata* is subshrubby with a well-developed short, woody trunk. These populations were distinguished from the more widespread subspecies *pinnata* and named subspecies *inyoensis* by Munz and Roos. Evidently these more woody plants are polyploid if our sampling of three populations is a fair indication of the situation in the subspecies as a whole. Our recent chromosome counts in *Stanleya* strongly indicate x = 14 as the fundamental number for the genus.

Strepthanthella

S. longirostris (Watson) Rydberg

$n = 14$: San Bernardino Co., California, Rollins 6705; Kern Co., California, Rollins 6725; Inyo Co., California, Rollins 6745; Clark Co., Nevada, Rollins 6709; Coconino Co., Arizona, Rollins 6782.

$n = 14$, $2n = 28$: Washington Co., Utah, Rollins 6790.

LITERATURE CITED

Böcher, T. W. 1951. Cytological and Embryological Studies in the Amphiapomictic *Arabis holboellii* complex. Dan. Biol. Skrifter **6**, no. 7, 1–59.

————————. 1954. Experimental Taxonomical Studies in the *Arabis holboellii* complex. Svensk. Botan. Tidskr. **48**: 31–44.

————————. 1969. Further Studies in *Arabis holboellii* and Allied Species. Botan. Tidsskr. **64**: 141–161.

Bolkhovskikh, Z. et al. 1969. Chromosome Numbers of Flowering Plants. V. L. Komarov Botanical Institute, Acad. Sci. USSR 1–926.

Green, P. S. 1962. Watercress in the New World. Rhodora **64**:32–43.

Hamel, J. L. 1951. Note sur le Noyau et les Chromosomes Somatiques du *Pringlea antiscorbutica* R. Br. ex Hook.f. Bull. Mus. Natl. Hist. Nat. **23**:548–551.

Manton, I. 1932. Introduction to the General Cytology of the *Cruciferae*. Ann. Bot. **46**: 509–556.

Mulligan, G. A. 1961. The Genus *Lepidium* in Canada. Madroño **16**: 77–90.

————————. 1965. Chromosome Numbers of the Family *Cruciferae* II. Canad. Journ. Bot. **43**: 657–668.

———————. 1968. Transfers from *Physaria* to *Lesquerella*. Canad. Journ. Bot. **46**: 527–530.

PAYSON, E. B. 1922. Species of *Sisymbrium* Native to America North of Mexico. Univ. Wyo. Publ. Sci. **1**:1–27.

RAVEN, P. H. ET AL. 1965. Chromosome Numbers of Spermatophytes, mostly Californian. Aliso **6**: 105–113.

ROLLINS, R. C. 1941a. A Monographic Study of *Arabis* in Western North America. Rhodora **43**: 289–325, 348–411, 425–481.

———————. 1941b. The Cruciferous Genus *Dryopetalon*. Contrib. Dudley Herb., Stanford **3**: 199–207.

———————. 1947. Generic Revisions in the *Cruciferae: Sibara*. Contrib. Gray Herb. Harvard. No. 165. 133–143.

———————. 1958. The Genetic Evaluation of a Taxonomic Character in *Dithyrea* (*Cruciferae*). Rhodora **60**: 145–152.

———————. 1966. Chromosome Numbers of *Cruciferae*. Contrib. Gray Herb. Harvard. No. 197. 43–65.

———————. 1969. A Remarkable New Crucifer from Mexico. Contrib. Gray Herb. Harvard. No. 198. 3–8.

———————. 1970. Notes on *Streptanthus* and *Erysimum (Cruciferae)*. Contrib. Gray Herb. Harvard. No. 200. 190–195.

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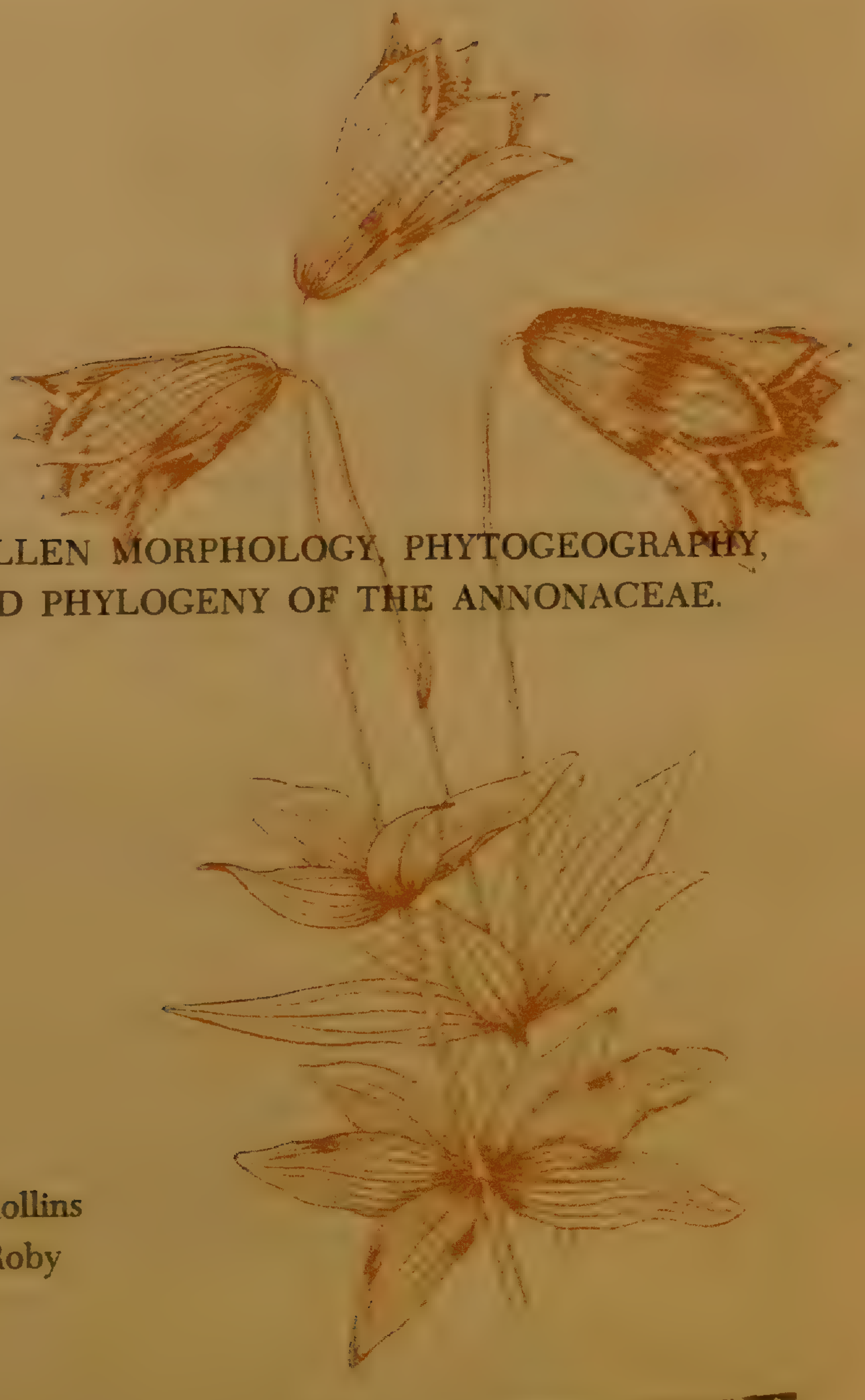

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POLLEN MORPHOLOGY, PHYTOGEOGRAPHY, AND PHYLOGENY OF THE ANNONACEAE[1]

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The *Annonaceae* is a moderate-sized family of flowering plants with approximately 130 genera and 2,300 species. Phytogeographically it is almost entirely tropical, with three main centers of distribution: the American tropics, tropical Africa, and the Asian tropics. Taxonomically it is quite distinctive with its rather primitive flowers typically having a three whorled, 3-merous perianth, numerous, extrorse, peltate stamens, numerous, distinct carpels, and seeds with ruminate endosperm. The primitive floral morphology is in sharp contrast to the more advanced wood anatomy, with all members of the family constantly possessing vessel elements with simple perforations (Vander Wyk & Canright, 1956). Phylogenetically, the *Annonaceae* were early recognized as primitive angiosperms with a close relationship to such families as the *Magnoliaceae* and the *Myristicaceae*.

While there has never been any serious question concerning the interfamilial phylogeny of the family, there has never been a satisfactory infrafamilial classification (cf., Sinclair, 1955; Fries, 1959; Hutchinson, 1964). All modern treatments of the family are rather artificial in that a single character of the floral morphology has been used to separate the family into two primary groups, the "Uvarieae" (with imbricate petals) and the "Unoneae" (with valvate petals). Attempting to understand the internal relationships of the family more clearly, the author made a preliminary survey of the pollen of some genera within the family and discovered not only that the pollen was often highly distinctive for certain genera, but that the pollen morphology of the taxa within the family was quite diverse and often indicative of relationships. The present study combines the results of an investigation of the pollen morphology of the family with data from floral morphology and phytogeography, hopefully to produce a natural infrafamilial classification of the *Annonaceae* and a better understanding of its internal phylogeny.

In the course of the present study a number of interesting discoveries were made—disulculate pollen, the primitive, distal aperture of *Pseudoxandra*, the peculiar, giant polyads of *Cymbopetalum*, etc.—but none was more surprising to the author than the realization that evidence from both palynology and floral morphology was overwhelmingly indicative of a New World (and/or possibly African) origin for the *Annonaceae*, in contrast to the great majority of "ranalean" families, which are clearly of an Asian or Australasian origin. (It appears as if cytotaxonomic data also

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suggest a New World origin for the family, cf., Ehrendorfer *et al.*, 1968.)

In the following, the floral morphology of the family is briefly surveyed. This is followed by a discussion of its pollen morphology and evolution, its phytogeography, and finally its phylogeny. The major discoveries made during the palynological investigation are listed in the summary at the end of the paper.

FLORAL MORPHOLOGY

The typical annonaceous flower consists of a calyx of three separate sepals; a biseriate corolla with six separate petals; numerous, spirally arranged, extrorse, peltate stamens; an apocarpous gynoecium of numerous, spirally arranged carpels with many to one ovules; baccate, more or less stipitate fruits; and seeds with a small embryo and an abundant, ruminate endosperm. There are, however, a number of interesting variations of this pattern within the family. Some genera have unisexual flowers; others may have lost one of the two whorls of petals, the six petals may be reduced to four, or the six may be in one whorl and be fused. Some genera have stamens that are not peltate, sometimes the stamens are few and whorled, or rarely staminodia are present as in *Uvaria, Anaxagorea,* and *Fusaea.* In some genera the carpels may be reduced to one, while in others they may be fused into a unilocular, compound pistil or multilocular syncarp. Very rarely the fruit may open at maturity, either as a dry follicle or as a ventrally or laterally dehiscing berry. Some genera have arillate seeds, while in the genus *Richella,* the seeds are winged. The most important recent papers dealing with the floral morphology of the family include Fries' revisions of the New World *Annonaceae* (1930–39), Sinclair's revision of the Malayan members of the family (1955), and the treatment of the *Annonaceae* by Le Thomas in the Flore du Gabon (1969). Floral characters that are particularly valuable in the classification of the family include peduncle bracts, inflorescence type and position, aestivation and nature of the petals, nature of the stamens, ovule number, and fruit type.

The peduncles of almost all members of the family are articulated (*Deeringothamnus* lacks an articulation). The bracts on the peduncle may be found in three basic arrangements: (1) bracts both above and below the articulation; (2) bracts only below the articulation; and (3) peduncle ebracteate.

The inflorescence may be axillary, leaf-opposed, terminal, supra-axillary, extra-axillary, or cauliflorous. Inflorescence position often has been used to separate closely related genera.

The imbricate versus valvate aestivation of the petals has been used classically to divide the family into two primary groups. However, it is quite evident that valvate petals have arisen independently within the family many times in different lines and that any basic separation of the family into two groups based solely upon petal aestivation is highly

artificial. The shape of the petals varies considerably, ranging from rounded to strap-shaped and even to clawed and mitriform. From character correlation it appears that the primitive petal shape is round, as in such putatively primitive genera as *Cremastosperma* and *Malmea* (cf., Diels, 1932). The texture of the petals is of some classificatory usefulness, e.g., *Hexalobus, Monodora,* and *Asimina* have membranous, often wrinkled petals, while the petals are thick and fleshy in *Annona* and related genera and in *Cymbopetalum* and its allies.

The staminal connectives have been used classically to order the genera into tribes. The most common type of stamen in the family is strongly peltate and its prevalence led Hutchinson (1964) to state that the "truncate anther-tips are a very striking feature of the *Annonaceae*, and they may represent an ancient relict type of leaf-structure." However, the primitive stamen type in the family is not peltate, as evident from the morphology of the microsporophylls in the genus *Anaxagorea*, clearly the most primitive type of stamen extant in the *Annonaceae*. In the least specialized species of the genus, *A. costaricensis*, the stamens are very laminar and leaf-like with a definite, stalk-like, basal section (pl. 20:1). The locules are widely separated (pl. 21:2) and the vascular trace terminally bifurcates and then recurves to bifurcate a second time (pl. 21:1). The overall appearance of these stamens is remarkably similar to those of *Degeneria*. However, it should be noted that, unlike the *Magnoliaceae* and *Degeneriaceae*, all stamens examined in the *Annonaceae* constantly exhibited a single trace (pl. 20:1). *Anaxagorea costaricensis* is the only exception because a few stamens in a flower may rarely have islands of vascular tissue. This undoubtedly represents the vestigial remains of the two lateral traces (pl. 20:2). In addition to other primitive features of the stamens of *Anaxagorea* is the occurrence, in several different species, of stomata on the abaxial, staminal surface (pl. 19:7–8).

The non-peltate stamens of other genera are probably secondary (e.g., *Miliusa, Orophea*). They are clearly secondary in the advanced, West Indian species of *Annona*. However, the non-peltate stamens in *Oxandra* may represent a primitive feature inasmuch as the genus has sulcate pollen and is found in the otherwise primitive *Malmea* tribe. A number of genera within the family are characterized by transversely septate anther locules at maturity. In this connection, it is interesting to note that some genera have rudimentary, sterile septa that are lost as the stamen matures (*Cananga, Monodora, Asimina,* and *Annona*—cf., Davis, 1966).

The low ovule number in a number of otherwise primitive genera (*Cremastosperma, Malmea, Pseudoxandra, Anaxagorea*), as well as the relatively few ovules in the closely related and generally less specialized family *Magnoliaceae*, argues for a low, basic ovule number for the family, with the possibility that a high ovule number may be secondary. Even assuming this, it is still clear that some genera may have secondarily acquired a low ovule number, e.g., *Annona*.

The overwhelming majority of the genera in the family have the apocarpous gynoecium developing into numerous, berry-like fruits. *Anaxagorea*, however, is unique with its dry, dehiscent follicles containing two seeds. They probably represent a primitive type within the family and are reminiscent of the fruit type in the *Magnoliaceae*. It might be noted that the related, but more specialized genus, *Xylopia*, has ventrally dehiscent, baccate fruits, possibly representing an intermediate fruit type between the follicles of *Anaxagorea* and the true indehiscent, baccate fruits of the great majority of the genera, as exemplified by *Cananga*. The fruit of *Cymbopetalum* is highly specialized in that it opens laterally, not along the ventral suture as in *Xylopia*, thus exposing its numerous, arillate seeds. The aril-covered seeds of *Cymbopetalum* and related genera are clearly highly specialized within the family and cannot be considered primitive.

POLLEN MORPHOLOGY

Previous Palynological Studies

Earlier studies generally included information on pollen as a matter of secondary interest. Mueller (1865–66) in his *Fragmenta Phytographiae Australiae* included illustrations of the pollen grains of *Ancana stenopetala=Fissistigma* in a plate along with flowers and fruits. Le Maout and Decaisne clearly illustrated a tetrad of *Asimina triloba* in their *System of Botany* (1876). Miquel, in Martius' *Flora Brasiliensis* (1856), evidently was the first to picture an annonaceous polyad as part of his plate of the genus *Hornschuchia;* it appears that no one has looked since for the occurrence of polyads within the family (Erdtman, 1945b, 1966).

In 1834 von Mohl noted the single aperture in the pollen grains of two undetermined species of *Annona* from Brazil. Observations covering a few species of *Annonaceae* were made by other classical workers in pollen morphology, such as Fritzsche and Fischer (cf., Erdtman, 1945b, 1966). Some embryological-cytological studies include information on pollen, the more important being those by Herms (1907), Lecomte (1896), Locke (1936), Periasamy and Swamy (1959), and Samuelsson (1914). Davis (1966) has summarized the embryological data known for the family. In 1952 Erdtman summarized the palynological data then known for the family. This included information on one or two species each for approximately 15 genera (Erdtman, 1966, pp. 49–50).

Vander Wyk (1950) included a study of the pollen of the family in his doctoral thesis, which was concerned primarily with vegetative anatomy. Although the section on wood anatomy was subsequently published (Vander Wyk & Canright, 1956), the pollen data were not. Vander Wyk investigated the pollen of 51 genera and 82 species. The study was based mainly on dry pollen from herbarium sheets re-expanded in lactic acid,

and included no acetylated material. He germinated pollen of *Asimina triloba* and found that the pollen tube emerged from the proximal surface. Also, he was of the opinion that the aperture in the family was proximal, not distal.

It is interesting to note that Agababyan (1967) found pollen germination in *Annona glabra*, *A. cherimola*, and *A. squamosa* to occur on either side of the grain, with usually 75–80 per cent of the grains germinating on the distal side even though that side was thicker. Further studies are certainly needed with living pollen, especially of the more primitive members of the genus, such as *Annona muricata*. Agababyan's statement, in the same paper, that the grains of *Annona* are not catasulcate but rather inaperturate, with the aperture being an artifact of acetolysis breaking the grains, is not borne out by the present comparative study of over 50 species of *Annona*.

The only modern, extensive survey of the pollen of the *Annonaceae* using acetylated grains is that by Canright (1963). For the purpose of comparison with the results of the present study, a critique of Canright's paper is given following the pollen descriptions in the present work.

MATERIALS AND METHODS

The present study includes a survey of 93 genera and approximately 430 species of *Annonaceae*. Fresh material was collected by the author in Mexico, Central America, Panama, Jamaica, and Colombia. Palynological material was also obtained from herbarium sheets in the following collections: Gray Herbarium, Harvard University (GH); Arnold Arboretum, Harvard University (A); New York Botanical Garden (NY); United States National Herbarium, Washington, D.C. (US); and the Field Museum of Natural History, Chicago, Illinois (F).

During the course of the study some 5,200 permanent slides of pollen samples and cleared stamens were prepared. A set is on deposit in the Paleobotanical Collections of the Botanical Museum of Harvard University. Each slide bears either my personal collection number[3] or my palynological accession number (with a "P" preceding the number). In the case of the latter, the original collector and his collection number are given in the citation of voucher specimens at the end of this study. All material studied and all slides made are vouchered and most of the herbarium specimens upon which this study is based have had their identity verified by the author from the available literature. In the case of the existence of abundant material of particular taxa, a deliberate attempt was made to use herbarium sheets which had been annotated by a specialist in the taxonomy of the family (such as Fries, Diels, *et al.*) or which were cited in a reliable flora or revisionary study.

[3]The author's first herbarium set is deposited in the Gray Herbarium of Harvard University.

Most of the pollen samples were prepared using Erdtman's (1960) standard acetolysis method with some modification. Rather than boiling the pollen samples, the majority of them were prepared by placing corked centrifuge tubes with pollen and standard acetolysis fluid in an oven overnight at 50–60°C. The material was then washed twice with glacial acetic acid and three times with water. Then the pollen was mounted in glycerine jelly. The use of disposable Pasteur pipettes was found helpful in transferring a mixture of pollen and glycerine jelly evenly to slides, especially when the available material was scanty.

In genera with highly reduced exine (all members of the *Guatteria* group, *Sapranthus*, and *Duguetia*), treatment with KOH was found necessary. Again, a corked centrifuge tube containing pollen material and varying concentrations of KOH (up to 1 N) was placed in an oven overnight at 50–60°C. The material was then washed in water 3–4 times, stained in basic fuchsin, toluidine blue, and/or alcian blue, and mounted in glycerine jelly. Tuf-On 74, made by Brooklyn Paint and Varnish Co., was used to seal all pollen mounted in glycerine jelly in order to make the slides permanent.

Stamens were cleared in KOH (up to 1 N) in Petri dishes in an oven at 50–60°C. Material was left in the oven until the desired amount of clearing was achieved. Then the stamens were dehydrated in an alcohol series, stained in basic fuchsin, cleared in xylene, and mounted in Permount. It was found that the easiest method to dehydrate and clear the stamens was to pipette the fluid out of the Petri dish with a disposable Pasteur pipette, leaving the stamens in the same dish throughout the entire process.

The KOH-treatment of pollen grains with reduced exine was found essential for the discovery and demonstration of the disulculate pollen types in the family, while the study of *in situ* pollen masses in the cleared stamens was necessary for the demonstration of tetrads and polyads in many genera where these structures are easily lost or damaged by acetolysis treatment (e.g., polyads breaking up into tetrad-like bodies, etc.).

The investigation was carried out with Zeiss Opton brightfield and Wild phase contrast microscopes. Photomicroscopy was through a Zeiss microscope, while Kodak High Contrast Copy Film and Adox KB-14 with Kodak Ektamatic paper and processing were used for the photomicrographs. A JSM-2 scanning electron microscope was used to obtain the scanning electronmicrographs.

Major Pollen Characters

The major features of pollen grains may be conveniently divided into different character-complexes including: (1) pollen-units (and their intrastaminal arrangement); (2) polarity; (3) symmetry; (4) apertures; (5) shape; (6) size; (7) exine structure and sculpturing. In the following, an attempt will be made to present the major concepts and the most important palynological terminology associated with each of the above

character-complexes, especially as related to the pollen of the *Annonaceae*. Most terminological usage follows that of Erdtman (1966). Different usage of terms or the introduction of terms other than those of Erdtman will be indicated where appropriate (e.g., the usage of the Faegri and Iversen term "columellae" for Erdtman's "infratectal bacula").

POLLEN-UNITS.[4] Most mature pollen grains are solitary (monads) within the thecal chambers of the stamen. However, in a number of angiosperm families the pollen grains at maturity are in dyads, tetrads, polyads (octads, 16's, etc.), massulae, or pollinia. A pollinium consists of the entire pollen-mass of a thecal chamber. The terms polyad and massulae have been used more or less interchangeably to denote pollen-units larger than tetrads but less than the entire pollen-mass of a thecal chamber. I believe that a useful distinction may be made between the two terms and would suggest using the term polyad for any pollen-unit larger than a tetrad but smaller than a pollinium in which the number of pollen grains is numerically ascertainable. I would restrict the term massulae to those pollen masses less than pollinia in which the number of individual grains is not ascertainable, due to very high number and/or a great degree of pollen fusion within the massula.

There are approximately 50 families of angiosperms (41 dicot and 12 monocot families) in which all or some members have pollen grains in tetrads or dyads (table 1). Of these, 13 have their pollen grains entirely or almost entirely in tetrads, eight have a significant number of genera with some or all species with tetrads, three have several genera with pollen in tetrads, and the remainder (26 families) have tetrads only very rarely. Dyads characterize two families (*Podostemaceae* and *Scheuchzeriaceae*), while the *Cyperaceae* have cryptotetrads (pseudomonads).

While tetrads occur in more than 50 families of angiosperms, polyads are quite rare. From a cursory survey of the literature, it appears that there are only five families in which polyads are known to occur: *Annonaceae*, *Leguminosae* (Sorsa, 1969), the genus *Hippocratea* of the *Hippocrateaceae* (Bartlett, 1967), *Asclepiadaceae*, and *Orchidaceae*. The latter two families are also the only angiosperm families with massulae and pollinia. Pollen tetrads may be of five different types (cf., Erdtman, 1945b). The most common among the angiosperms as a whole is the tetrahedral tetrad, but among the primitive monosulcate dicots and the monocots, the most common is the tetragonal or square tetrad with the rhomboidal tetrad less common. The decussate or cross tetrad, and especially the linear tetrad, are of rather infrequent occurrence.

While the majority of genera of the *Annonaceae* have solitary pollen grains at maturity (pl. 1:1–2; 8:4; 10:3; 21:2; 45:1,2,5), some 20 genera have their pollen grains in tetrads (table 2). Of these, one *(Xylopia)* also has a few species with polyads, while another *(Annona)* has a few with solitary grains. All species of the other 18 genera were found to have

[4]A pollen-unit is the grouping in which pollen is found at maturity within the stamen, i.e., whether in monads (solitary), tetrads, polyads, etc.

tetrads consistently. The most common type of tetrad within the *Annonaceae* is the tetragonal tetrad (pl. 23:3; 31:2–3; 32:1,4; 42:5; 46:1). Genera with tetragonal tetrads frequently have some rhomboidal tetrads also. Three genera *(Pseudoxandra, Mitrephora,* and *Pseuduvaria)* exhibit markedly tetrahedral tetrads (pl. 1:3; 15:4,7). These genera may occasionally have tetragonal (pl. 13:6; 15:5), rhomboidal (pl. 15:3,6), or decussate tetrads also. No examples of linear tetrads were observed in the family.

TABLE 1. ANGIOSPERM FAMILIES WITH POLLEN-UNITS OTHER THAN MONADS†

DICOTYLEDONAE

Magnoliidae
- Lactoridaceae***
- Winteraceae***
- Annonaceae** (also polyads)
- Monimiaceae
- Nymphaeaceae
- Berberidaceae
- Papaveraceae

Hamamelidae
- Myrothamnaceae***
- Eucommiaceae

Caryophyllidae
- Didiereaceae (possibly tetrads)

Dilleniidae
- Sarcolaenaceae***
- Actinidiaceae
- Guttiferae
- Tiliaceae
- Nepenthaceae***
- Droseraceae***
- Begoniaceae
- Datiscaceae
- Cucurbitaceae
- Ericaceae***
- Epacridaceae**
- Empetraceae***
- Pyrolaceae***

Rosidae
- Saxifragaceae
- Rosaceae
- Leguminosae** (also polyads)
- Podostemaceae** (dyads, possibly polyads)
- Onagraceae*
- Cornaceae
- Rafflesiaceae
- Hippocrateaceae (polyads)
- Celastraceae
- Sapindaceae

Asteridae
- Gentianaceae**
- Apocynaceae**
- Asclepiadaceae** (also polyads, massulae, and pollinia)
- Solanaceae
- Bignoniaceae*
- Pedaliaceae
- Hydrostachyaceae***
- Goodeniaceae
- Rubiaceae*

MONOCOTYLEDONAE

Alismatidae
- Hydrocharitaceae
- Scheuchzeriaceae*** (dyads)

Commelinidae
- Juncaceae***
- Thurniaceae***
- Cyperaceae*** (cryptotetrads or pseudomonads)
- Typhaceae***
- Bromeliaceae

Arecidae
- Araceae

Liliidae
- Philydraceae
- Amaryllidaceae
- Velloziaceae**
- Orchidaceae** (also polyads, massulae, and pollinia)

†Based mostly on data of Erdtman, 1945b, 1966; families arranged according to Cronquist (1968); tetrads present unless otherwise indicated; *** all members or the overwhelming majority have pollen in tetrads or dyads; ** a significant number of genera have pollen in tetrads or dyads; * several genera have pollen in tetrads or dyads; no mark indicates tetrads or dyads are very rare or may only be found in certain individual plants of a species (e.g., pollen tetrads the author found in material from one particular tree of *Eucommia*).

TABLE 2. GENERA OF ANNONACEAE WITH TETRADS, POLYADS, AND SEPTATE STAMENS

TETRADS

Pseudoxandra, Mitrephora, Pseuduvaria, Neostenanthera, Xylopia (some polyads), Duckeanthus, Fusaea, Meiocarpidium, Cananga, Goniothalamus, Richella, Uvariastrum, Uvariopsis, Hexalobus, Monodora, Diclinanona, Asimina, Deeringothamnus, Annona (some solitary grains), Raimondia

POLYADS

Xylopia (mostly tetrads), Cymbopetalum (octads), Cardiopetalum (octads), Porcelia (polyads up to 24's), Trigynaea (octads), Hornschuchia (polyads of 16's), Disepalum (octads)

SEPTATE STAMENS

Neostenanthera, Xylopia, Goniothalamus, Richella, Cymbopetalum, Cardiopetalum, Porcelia, Trigynaea, Hornschuchia

Six genera were found to have polyads in all species examined (table 2). A seventh *(Xylopia)* has a few species with polyads (pl. 23:6; 25:1), although the majority of the species in this genus have tetrads (pl. 23:3,5; 24:3; 25:2). Of the six genera constantly with polyads, four have octads (pl. 48:5,6; 50:6; 51:5–6; 52:5), one has polyads of 16 grains, and one has polyads of 16, 18, 20, 24, etc. (pl. 49:3–4). The polyads of some species of *Xylopia* are distinctive, usually consisting of about 5–6 individually discernible tetrads, while those in the other genera are more or less irregular with no individual tetrads visible. Since the polyads in *Porcelia* may be in multiples other than four, it would be interesting to investigate microsporogenesis and pollen formation in this genus.

Nine genera of *Annonaceae* have transversely locellate anthers at maturity (table 2). Five of these have polyads, three have tetrads, and one *(Xylopia)* has both tetrads and polyads, depending on the species. All genera with polyads were found to have septate stamens at maturity except *Disepalum*. The tetrads or polyads in the genera with septate stamens are each in a separate compartment within the stamen (pl. 25:1; 30:2; 48:4; 49:5–6). It is of interest to note that the polyads in the subfamily *Mimosoideae* of the *Leguminosae* are also separated by septa within the anther locule (cf., Maheshwari, 1950).

POLARITY. The polarity of a pollen grain is of special importance in determining aperture type and hence grain homologies. The determination of grain polarity in genera or species with tetrads at maturity is quite straightforward. In taxa with solitary grains, however, the correct determination of polarity may be somewhat more difficult—one must either rely on comparative studies of related taxa with permanent tetrads or study cytologically the development of the immature pollen tetrad before the grains separate to determine grain polarity with respect to apertures.

The polar axis of a pollen grain is that line passing through the center of the grain from the outside to the center of the tetrad (or to the center of the tetrad at the time of its formation in the case of solitary grains).

The equatorial axis perpendicularly bisects the polar axis and forms the boundary between the distal and proximal poles of the grain. The distal pole faces away from the tetrad, while the proximal pole is directed inward, facing the center of the tetrad. The two major types of grain polarity are apolar (without discernible poles once the grains are not in tetrads) and polar (with distinct poles). Polar grains may be further subdivided into isopolar (with the equatorial plane dividing the grain into equal halves) and heteropolar (with the polar faces markedly dissimilar). The pollen grains of the *Annonaceae* may be apolar (the inaperturates, pl. 7:9), isopolar (the disulculates, pl. 17:7), or heteropolar (the sulcates and ulcerates, pl. 1:4; 61:1–2).

SYMMETRY. Symmetry (as well as polarity) is largely determined by apertures. The two major types are radiosymmetry and bilateral symmetry. Radiosymmetric pollen grains have more than two vertical planes of symmetry (or if only two such planes, then the equatorial axes are equilong). Bilateral grains have only two vertical planes of symmetry and the equatorial axes are not equilong.

In the *Annonaceae*, all the inaperturates are radiosymmetric, while all the sulcates and ulcerates are bilateral. The disulculates may be either radiosymmetric (pl. 17:6; 18:1) or bilateral (pl. 17:7–8, 10–12; 18:2–4), depending on whether the equatorial axes are equilong or not. The genus *Pseudoxandra* is asymmetric-fixiform because of the irregular shape of the grains due to the frequent occurrence of random protuberances of the exine.

APERTURES. Apertures are openings or thin areas in the exine through which the pollen tube usually emerges at the time of germination. The evolution of apertures in pollen grains was one of the major advances of the seed plants and the aperture type is one of the most important phylogenetic characters of pollen grains (cf., table 3). Pteridophytes, in the strict sense, do not have apertures. However, they do have non-homologous, thin areas by which the spores often open. These are the tetrad scars, which may be trilete (triradiate) or monolete (with one linear scar).

It was in gymnospermous plants that the first apertures evolved. Certain fossil gymnosperm pollen (e.g., the pteridosperms) still has a trilete scar on the proximal face which is homologous to the trilete scar of pteridophyte spores. The first true apertures, however, evolved at the distal pole and were furrow-like. The palynological term for an elongate, polar aperture is a sulcus and since these first apertures were at the distal (ana-) pole, these grains are known as anasulcate. Most modern gymnosperms are still anasulcate, although some other developments have occurred, such as the formation of air bladders, the secondary loss of the aperture to become inaperturate, etc.

In the course of the evolution of the flowering plants a new and fundamentally different type of aperture arose, the colpus. This furrow-like aperture is not polar but equatorial (being perpendicular to the equator

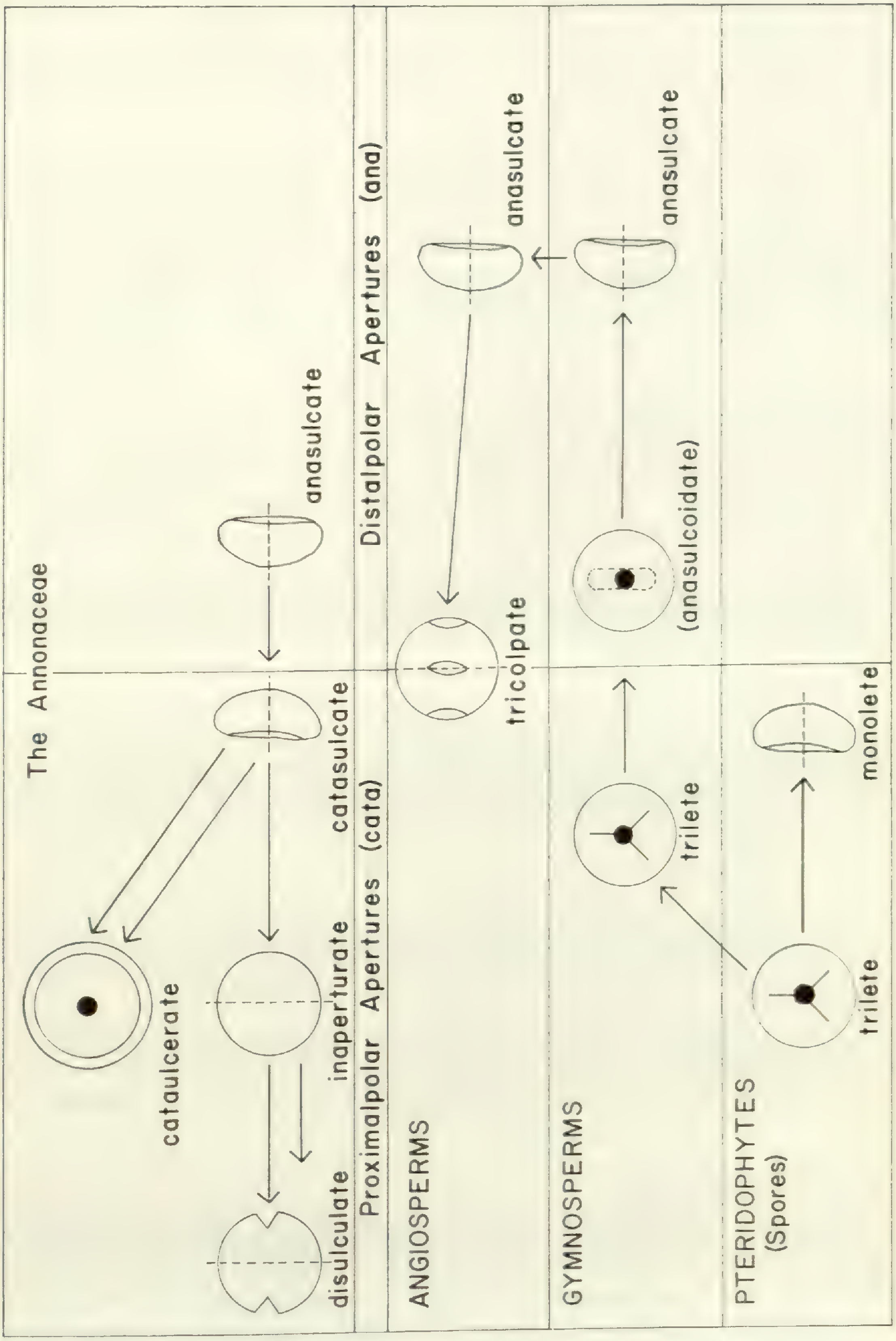


TABLE 3. POLLEN APERTURE EVOLUTION IN THE VASCULAR PLANTS AND WITHIN THE FAMILY ANNONACEAE

of the grain). The basic angiosperm pattern has three of these equatorial apertures and the grains are known as tricolpates. However, some of the primitive dicot families such as the *Magnoliaceae, Degeneriaceae,* etc. (including the monocots) have retained the primitive anasulcate type of pollen which is so prevalent among the gymnosperms.

One of the earliest concepts developed in comparative pollen morphology, which later became almost a dogma, was that the furrow in sulcate pollen grains was always at the distal pole and hence the grains were always anasulcate. This concept was promulgated by Wodehouse (1935, p. 324) in his classic book on pollen grains. The validity of this hypothesis for annonaceous pollen was first questioned by Bailey and Nast (1943). Since then, the true nature of the annonaceous aperture has been open to some question (Erdtman, 1966; Canright, 1963; Kuprianova, 1967). From a study of the more than 20 annonaceous genera in which tetrads or polyads occur, it is quite clear that in all genera except one the aperture is on the proximal (cata-) pole (pl. 23:4; 30:4; 50:6), and not the distal pole as in all other known monosulcate grains, indicating that the family *Annonaceae* is unique in having catasulcate pollen.

The genus *Pseudoxandra* is of special interest because some of its species have retained the primitive anasulcate condition characteristic of many of the other "ranalean" dicots. Even more noteworthy is the fact that within the genus the complete transition from anasulcate to catasulcate may be observed. The pollen of *Pseudoxandra coriacea* has a well-defined distal sulcus (pl. 1:3; 57:1), while the distal sulcus of *P. guianensis* has somewhat weaker margins. *Pseudoxandra leiophylla* and *P. polyphleba* are transitional from anasulcate to catasulcate (pl. 2:5), while *P. williamsii* has a well-defined, proximal aperture (pl. 2:6). *Pseudoxandra coriacea* is also remarkable in being the only species of the *Annonaceae* examined to have some trichotomosulcate grains (pl. 1:4; 57:1). Since *Pseudoxandra* is the only genus to have permanent tetrads among a group of related genera having sulcate pollen (the "*Malmea* tribe"), it is difficult to determine with certainty the orientation of the sulcus in these other genera (*Malmea, Cremastosperma, Unonopsis,* etc.). However, in view of the rare occurrence of catasulcate tetrads in *Cremastosperma cauliflorum* (cf., Canright, 1963), it is probably best to consider these genera as having catasulcate pollen unless proved otherwise through the cytological study of pollen development.

The sulcate pollen grains within the family have a fairly wide range of diversity (cf., pl. 2:1,7–8; 3:1,4–5,7,10–12; 4:1–7; 5:1–4,6,8; 10:4–6; 19:2; 22:1–3). In a large number of genera the aperture has been lost and the grains have become inaperturate (pl. 8:1–6; 9:3–12; 12:1–12; 13:1–6; 17:1–5; 32:6–9; 44:1–7). In two genera which are characterized mainly by inaperturate pollen (*Uvaria* and *Artabotrys*), a few species show the vestigial remains of a reduced sulcus (pl. 9:1; 14:3,4). Another type of aperture in the *Annonaceae* is found in two different groups and presumably arose independently through parallel evolution from inaperturate

pollen. This disulculate pollen type was previously unknown for the family. A sulculus is a furrow-like aperture found on the equator of the grain and parallel to it. It should not be confused with the colpus, which is also equatorial but perpendicular to the equator. The colpate and derived types of pollen characterize the majority of angiosperms (all the higher dicots), while the sulculate type is restricted to some of the primitive "ranalean" dicots and the monocots.

The two groups with disulculate pollen are the genus *Sapranthus* (pl. 17:6–7; 18:1–4), which is closely related to some genera with inaperturate pollen *(Desmopsis, Stenanona, Reedrollinsia),* and the closely related genera *Guatteria, Guatteriopsis,* and *Heteropetalum* (pl. 17:8–12; 18:5–6). The latter genera form a natural group, the "*Guatteria* tribe."

Finally, in some genera the catasulcus has been modified (apparently twice in two parallel lines) into a rounded, pore-like aperture. Such a polar aperture is known as an ulcus and since, in the *Annonaceae,* this rounded aperture is on the inner face, the grains are known as cataulcerate (cf., pl. 26:3; 28:1,3,5; 29:1–5; 53:5; 59:3). Thus, with reference to aperture type, the pollen of the *Annonaceae* may be anasulcate, anatrichotomosulcate, catasulcate, cataulcerate, inaperturate, or disulculate. (Grains in which the orientation of a polar furrow is unknown may be referred to simply as sulcate.)

SHAPE. The shape of a pollen grain is usually correlated with the type of aperture, e.g., tricolpates tend to be globose to elliptic, while monosulcates tend to be boat-shaped. The method and length of pollen preparation may cause the shape of monosulcate grains to vary considerably (cf., pl. 19:2,3). Pollen in the *Annonaceae* ranges from boat-shaped (pl. 2:8; 3:1; 5:1–3), oblong-elliptic (pl. 17:7–8,10–12; 18:2–6), or triangular (pl. 22:4,6; 24:1–2, 4–5), to disc-like, concave-convex (pl. 23:1; 28:3,5) or rounded (pl. 36:1,5; 38:3; 46:4; 47:1,4) to globose (pl. 7:6,9,10; 8:1–6; 13:1–6; 32:6–9; 44:1–7).

SIZE. The size of pollen grains is greatly affected by the method of preparation and hence is a most unreliable character. Order of magnitude, based on defined size classes, is probably the single most useful measurement of pollen grains. The following size classes, based on the length of the longest grain axis (exclusive of spines in echinate grains), have been adopted, following Erdtman (1945a):

Very small grains	$<10\mu$
Small grains	$10–25\mu$
Medium-sized grains	$25–50\mu$
Large grains	$50–100\mu$
Very large grains	$100–200\mu$
Gigantic grains	$>200\mu$.

The length averages of the grains of different species of annonaceous pollen range from $23–283\mu$, while similar average lengths for all species of each genus as a unit range from $24–183\mu$ (table 4). Thus, in terms of size classes, pollen in the family ranges from small to gigantic. The

average long axis grain measurement for the family is 60μ. Genera with average long axes measurements of less than 30μ include *Cleistochlamys* (pl. 32:6–9), *Enneastemon* (pl. 7:6), *Stelechocarpus* (pl. 9:11), and *Monanthotaxis* (pl. 6:5). Genera with grains having an average long axis of more than 100μ include *Cananga* (pl. 26:3), *Asimina* (pl. 34:3–6), *Annona* (pl. 33:5), *Cardiopetalum* (pl. 50:1–2), *Fusaea* (pl. 26:1; 27:1), *Duckeanthus* (pl. 26:2), and *Cymbopetalum* (pl. 47:1–6). *Cymbopetalum* has by far the largest pollen in the family. The long axis average for the genus is 183μ and the averages for the different species range from 130–283μ. Some individual grains of *Cymbopetalum odoratissimum* reach 350μ, probably the largest recorded fixiform pollen in the angiosperms (pl. 47:1–3; 59:3; 60:3–5; 61:1–2).

EXINE STRUCTURE AND SCULPTURING. The pollen wall (sporoderm) consists of two fundamentally different layers: an inner, more or less cellulosic layer (cf., Faegri and Iversen, 1964) which is destroyed upon acetylation (the intine); and an outer, highly resistant layer, composed of so-called sporopollenins (the exine). Since most modern pollen is prepared for study by acetolysis and the intine is lacking in fossil pollen, for all practical purposes the study of pollen morphology consists of the study of the exine.

The exine typically consists of two layers: an inner, basal layer or nexine (nonsculptured exine); and an outer, sculptured layer or sexine (sculptured exine). The basic element of the sexine may be thought of as a drumstick-shaped rod (pilum) with a rod-like basal part (baculum of Erdtman, columella of Faegri and Iversen) and a swollen head (caput). If the heads of the pila fuse, a roof-like structure called the tectum is formed and the grain is tectate. If perforations develop in the roof, the grain is tectate-perforate. If the columellae are locally free from the nexine and form folds to make the exine appear wavy, the grains are subsaccate. If the folds are extremely well-developed and run entirely around the grain, the pollen is perisaccate. Grains with free pila not fused by their heads are intectate, while those with the pila laterally fused into a reticulate pattern but without the formation of a roof are semitectate.

A very important concept in the morphology of pollen exine is the difference between structure and sculpturing. In intectate and semitectate grains, the pila comprise both the structure and the sculpturing. However, in tectate grains the possibility exists for other elements to be formed on the roof of the tectum, which are then considered to be the sculpturing. In tectate grains the structure is formed by the columellae (infratectal bacula), which are enclosed by the tectum.

The most important palynological distinction between a photomicrograph and a scanning electronmicrograph is that the latter shows only the sculpturing (pl. 60:3–5), while the former shows both structure and sculpturing (pl. 61:2) due to the penetration of light waves and the ability of the light microscope to produce optical sections.

TABLE 4. SIZES IN MICRONS OF ANNONACEOUS POLLEN

SMALL GRAINS 10–25μ

24 Cleistochlamys*
25 Enneastemon

MEDIUM-SIZED GRAINS 25–50μ

26 Stelechocarpus
28 Monanthotaxis
32 Ellipeia, Woodiella, Neouvaria
33 Platymitra, Pseudephedranthus Popowia (African)
34 Mezzettia
35 Pseuduvaria, Popowia
36 Mitrella
39 Ruizodendron, Oxandra, Sageraea, Oncodostigma
40 Guamia
41 Onychopetalum, Anomianthus, Dasymaschalon, Fissistigma
42 Cleistopholis, Miliusa, Friesodielsia
43 Enicosanthum
44 Polyalthia, Bocageopsis, Tetrameranthus
45 Desmos, Orophea
48 Stenanona, Chieniodendron, Papualthia
49 Duguetia, Meiogyne, Trivalvaria, Rollinia

LARGE GRAINS 50–100μ

50 Rolliniopsis, Ephedranthus, Tetrapetalum, Reedrollinsia
51 Saccopetalum, Artabotrys
52 Sapranthus, Desmopsis
53 Alphonsea
54 Polyceratocarpus, Friesodielsia (African)
55 Mitrephora
56 Uvariopsis
57 Uvaria, Phaeanthus
58 Isolona
60 Hexalobus
62 Cyathostemma, Uvariastrum
63 Heteropetalum
64 Enantia, Trigynaea
65 Cyathocalyx, Monodora
66 Drepananthus
67 Melodorum, Piptostigma, Raimondia
69 Unonopsis
70 Anaxagorea, Guatteriopsis
71 Richella, Pseudoxandra
73 Neostenanthera
77 Rauwenhoffia
80 Cremastosperma
81 Monocarpia, Malmea
84 Hornschuchia
87 Xylopia
90 Guatteria, Porcelia
93 Diclinanona
95 Goniothalamus
96 Disepalum, Meiocarpidium
97 Deeringothamnus

VERY LARGE GRAINS 100–200μ

102 Cananga
104 Asimina
107 Annona
108 Cardiopetalum
115 Fusaea
141 Duckeanthus
183 Cymbopetalum

*Average long axis measurement of all grains of all species for each genus.

The most widely used sculpturing terms are the following:

psilate (smooth)
foveolate (pitted)
fossulate (grooved)
scabrate (with very fine projections)
gemmate (with sessile pila)
clavate (pilate)
verrucate (warty)
baculate (with rod-like sculpturing elements with no swollen heads as in the clavate forms)
echinate (spiny)
ornate or rugulate (with elongate sculpturing elements irregularly distributed)
striate (with elongate sculpturing elements more or less parallel)
striato-reticulate (with elongate sculpturing elements parallel to reticuloid)
reticulate (with sculpturing elements forming a reticular pattern)

The pollen of the *Annonaceae* is basically tectate with one notable exception, the genus *Trigynaea*, which is the only definitely intectate member of the family (pl. 44:12; 50:5; 52:1–2; 53:1–2). Obviously discernible perforations occur in the tectum of over 20 genera (table 5). A

number of genera have their exine and/or columellae so reduced as to make determination of their tectate nature impossible from light microscope studies alone. These genera have been described as microtectate (table 5), since in all instances they apparently can be derived from related groups that have a definite tectum. Pollen studies using the transmission electron microscope would be very useful here. In a number of these genera, the columellae are probably so reduced that the sexine and nexine may appear simply as two electron-distinct layers. A few subsaccate (pl. 4:7) to perisaccate (pl. 4:1–5) grains were observed in the family (table 5).

The columellae may be extremely well-developed (pl. 47:1–3) to moderately well-developed (pl. 3:2) to reduced (pl. 5:7) to indiscernible (pl. 23:3–4). They may be random and solitary (pl. 38:3) to fused laterally into arcs, etc., forming an ornate pattern (pl. 40:1–4), to reticulate (pl. 2:8–12; 37:1–2).

The exine may be extremely thick (pl. 27:2; 49:1–2) to extremely reduced (pl. 17:8–12). In some of the cataulcerate forms the exine may be more or less wanting on the entire inner face of the grain (pl. 23:1; 34:6; 47:4–5; 53:5; 59:3; 61:1).

The sculpturing runs the gamut from psilate (pl. 7:11) to foveolate (pl. 27:4–6) to fossulate (pl. 57:2) to gemmate (pl. 13:4) to clavate (pl. 44:12; 50:5) to verrucate (pl. 15:7; 58:3–5) to baculate (pl. 53:1–2) to echinate (pl. 7:1–5). Ubisch bodies are very conspicuous in certain genera (pl. 59:1–2,4–5).

Generic Pollen Descriptions

In the following section, formal pollen descriptions are given for some 92 genera of *Annonaceae* (the description of *Saccopetalum* is included with that of *Miliusa*). The format is the same throughout. First, the type of pollen-unit (whether solitary grains, tetrads, or polyads) is given, then the polarity and symmetry. This is followed by the type of aperture, the shape of the grain, then the size class using the size groups outlined above. The range of the long axis averages is taken from the average of the shortest grains and the average of the longest grains for all the species of the genus examined. Usually they are based on five or more grains for each species. The genus average is derived from the averages for all the species of the genus studied. The averages for the tribes, subfamilies, and the family are derived from the averages of the genera in each taxonomic category. Finally, the exine structure and sculpturing is discussed. At the end of each pollen description the number of species examined out of the total number of species in the genus is recorded, including a list of the plates illustrating the pollen of each genus.

The particular species examined in each genus may be found by referring to the citation of voucher specimens in the appendix at the end of the work. The genera in this list are arranged in the same order as they are treated in the formal descriptions, with the species arranged alpha-

TABLE 5. GENERA OF ANNONACEAE WITH PRONOUNCED TECTATE-PERFORATE, MICROTECTATE, AND SUBSACCATE OR PERISACCATE POLLEN EXINE

TECTATE-PERFORATE

Cremastosperma, Malmea, Ephedranthus, Pseudephedranthus, Pseudoxandra (reduced), Unonopsis, Bocageopsis, Enantia, Uvaria bipindensis, Polyalthia (the 2 sulcate spp.), Monocarpia, Cyathocalyx, Uvariastrum, Uvariopsis, Hexalobus, Monodora (not very prominent), Diclinanona, Asimina, Deeringothamnus, Annona, Raimondia, Cymbopetalum, Cardiopetalum, Porcelia, Hornschuchia, Disepalum

MICROTECTATE

Tetrameranthus, Monanthotaxis, Enneastemon, Popowia (African), Desmos, Dasymaschalon, Friesodielsia, Guatteria, Guatteriopsis, Heteropetalum, Anaxagorea, Piptostigma, Neostenanthera, Xylopia, Duckeanthus, Fusaea, Meiocarpidium, Cananga, Goniothalamus, Richella

SUBSACCATE OR PERISACCATE

Subsaccate:
Oxandra (slightly in some spp.), Ruizodendron (prominently), Bocageopsis (slightly)
Perisaccate:
Onychopetalum (prominently)

betically under the genus. An alphabetical index to the generic descriptions is to be found at the end of this paper, and, when used in conjunction with the listing of plates after each description, serves as an index to the photomicrographs.

The genera are arranged according to the proposed subfamilial and tribal groupings. The format of the data given for each genus is repeated at the tribe, subfamily, and family levels so that one may readily acquire an idea of the distinguishing palynological characters of these higher taxonomic categories.

ANNONACEAE

POLLEN MORPHOLOGY: Pollen grains solitary (most of the *Malmea* subfamily) or in tetragonal, rhomboidal, tetrahedral, or rarely decussate tetrads or in polyads (most of the *Fusaea* and *Annona* subfamilies). Stamens sometimes transversely septate, with each tetrad or polyad in a separate compartment (the *Cymbopetalum* tribe except *Disepalum*, and in *Xylopia, Neostenanthera, Goniothalamus*, and *Richella* of the *Fusaea* subfamily). Heteropolar, apolar, or isopolar and bilateral or radiosymmetric (rarely asymmetric-fixiform). Anasulcate (*Pseudoxandra* spp.), rarely anatrichotomosulcate (*Pseudoxandra coriacea*), sulcate (the *Malmea* tribe), catasulcate or cataulcerate (most of the *Fusaea* and *Annona* subfamilies), inaperturate (most of the *Uvaria* tribe), or disulculate (the *Guatteria* tribe and the genus *Sapranthus* of the *Uvaria* tribe). Boat-shaped, oblong-elliptic, triangular, disc-like, concave-convex, rounded, or globose. Small to gigantic, long axis measurement averages for the species 23–283μ, for the genera 24–183μ, for the family 60μ (up to 350μ in some grains of *Cymbopetalum odoratissimum*). Tectate-perforate to tectate to microtectate, rarely intectate (*Trigynaea* of the *Cymbopetalum* tribe),

columellae extremely well-developed (*Annona* subfamily) to well-developed (*Malmea* and *Uvaria* tribes) to reduced to indiscernible (*Fusaea* subfamily, *Guatteria* tribe), random and solitary to fused laterally into arcs, etc. and ornate to reticulate. Exine surface psilate, foveolate, fossulate, scabrate, gemmate, clavate, verrucate, baculate, echinate, subsaccate, or perisaccate. Exine extremely thick (*Fusaea* and *Annona* subfamilies) to highly reduced (*Guatteria* tribe, *Sapranthus*, and *Duguetia*), frequently more or less entirely wanting on the inner face (in most members of the *Annona* subfamily and in many members of the *Fusaea* subfamily).

Number of genera examined: 93 out of ca. 130.
Number of species examined: 430 out of ca. 2,300.

Pseudoxandra is notable for showing the transition from anasulcate to the catasulcate (or cataulcerate) grains which characterize the great majority of the members of the *Fusaea* and *Annona* subfamilies. Most of the pollen of the genera in the latter two subfamilies is in tetrads or polyads, while only three genera (*Pseudoxandra*, *Mitrephora*, and *Pseuduvaria*) of the *Malmea* subfamily have pollen grains in tetrads. The *Malmea* tribe is entirely sulcate, the *Uvaria* tribe is almost entirely inaperturate (rarely sulcate or disulculate), and the *Guatteria* tribe is entirely disulculate. The *Fusaea* subfamily is characterized by cataulcerate grains in tetrads without discernible columellae, while the *Annona* subfamily has mostly cataulcerate grains in tetrads or polyads with extremely well-developed columellae. Both the *Fusaea* and *Annona* subfamilies show pollen gigantism, a high number of genera with tetrads or polyads, and a number of genera with septate stamens with each tetrad or polyad in a separate compartment. The extremely reduced exine of the genera in the *Guatteria* tribe and the almost total lack of exine on the proximal face of the grains of members of the *Cymbopetalum* tribe are noteworthy.

THE MALMEA SUBFAMILY

Pollen Morphology: Pollen grains solitary (rarely in tetrahedral tetrads in *Pseudoxandra*, *Mitrephora*, and *Pseuduvaria*). Heteropolar and bilateral (*Malmea* tribe), apolar and radiosymmetric (most of the *Uvaria* tribe), or isopolar (the *Guatteria* tribe). Sulcate (the *Malmea* tribe and a few species of the *Uvaria* tribe), inaperturate (most of the *Uvaria* tribe), or disulculate (the *Guatteria* tribe and *Sapranthus*). Boat-shaped to globose to oblong-elliptic. Medium-sized to large (rarely small), long axis measurement averages for the genera 25–81μ, average for the subfamily 59μ. Tectate-perforate to tectate to microtectate, columellae distinct to reduced to indiscernible, random to reticulate, exine surface psilate, gemmate, verrucate, baculate, or echinate, infrequently subcaccate to perisaccate, exine sometimes highly reduced (the *Guatteria* tribe, *Sapranthus*, and *Duguetia*).

Pseudoxandra is the only genus in the family with some species that are

definitely anasulcate, rather than catasulcate or cataulcerate, as is the case with all other genera in the family in which the position of the polar aperture is known. *Pseudoxandra*, *Mitrephora*, and *Pseuduvaria* are the only genera in this subfamily with tetrads. *Desmos*, *Dasymaschalon*, and *Friesodielsia* are very distinctive with their strongly echinate sculpturing. The *Malmea* tribe is entirely sulcate, while the great majority of the genera of the *Uvaria* tribe have inaperturate grains. The *Guatteria* tribe are all disulculate, with *Sapranthus* (in the *Uvaria* tribe) being the only other disulculate genus in the family. The *Guatteria* tribe is remarkable for its extremely reduced exine.

THE MALMEA TRIBE

POLLEN MORPHOLOGY: Pollen grains solitary, rarely in tetrads *(Pseudoxandra)*. Heteropolar, bilateral (rarely asymmetric-fixiform in *Pseudoxandra*). Sulcate, rarely trichotomosulcate *(Pseudoxandra coriacea)*. Boat-shaped. Medium-sized to large, long axis measurement averages for the genera 39–81μ, average for the tribe 59μ. Tectate-perforate to tectate, columellae distinct, well-developed to reduced, random to reticuloid to reticulate. Grains occasionally more or less subsaccate to perisaccate *(Oxandra, Ruizodendron, Bocageopsis, Onychopetalum)*.

Pseudoxandra is very important palynologically because of the transition within the genus from anasulcate to catasulcate pollen.

Pseudoxandra R. E. Fries

POLLEN MORPHOLOGY: Pollen grains in tetrahedral tetrads (occasionally tetragonal or decussate), longest tetrad axis 77–104μ. Heteropolar, sometimes asymmetric-fixiform because of the irregular shape of the grain due to frequent occurrence of random exine protuberances. Anasulcate with the sulcus frequently curved *(P. coriacea, P. guianensis)* to transitional-catasulcate *(P. leiophylla, P. polyphleba)* to catasulcate *(P. williamsii)*, frequently anatrichotomosulcate *(P. coriacea)*, slightly subsaccate near the aperture margin in some of the catasulcate forms, as found in *Cananga*. Boat-shaped with oblong, elliptic, rounded or triangular AMB.[5] Large grains, longest axis 68–78μ, average 71μ. Tectate, columellae random to loosely ornate to reticuloid, distinct but somewhat reduced. Sculpturing (in *P. coriacea*) fossulate, tectate-perforate.

Number of species examined: 5 out of 6. Plates: 1:3–5; 2:5–6; 57:1–2.

Cremastosperma R. E. Fries

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped with elliptic to oblong AMB. Large grains, longest axis 63–95μ. average 80μ. Tectate-perforate, columellae random, reticuloid, or reticulate. distinct and well-developed (very prominent and highly characteristic in *C. anomalum*).

Number of species examined: 9 out of 17. Plates: 3:1–6.

Malmea R. E. Fries

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped with rounded, oblong, or elliptic AMB. Large grains, longest axis 67–93μ, average 81μ. Tectate-perforate, columellae random to highly reticulate. distinct and well-developed. Sculpturing (in *M. costaricensis*) psilate with medium-sized tectal perforations.

Number of species examined: 8 out of 14. Plates: 1:1; 2:1–4,7–12; 57:3–4.

[5]AMB is the outline of a pollen grain one sees when the polar axis is directed towards the observer; it may or may not coincide with the equator of the grain.

Ephedranthus S. Moore

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped. Medium-sized to large, longest axis 43–58μ, average 50μ. Tectate-perforate, columellae random to reticuloid to reticulate, distinct and well-developed.

Number of species examined: 2 out of 4. Plates: 3:8–9.

Pseudephedranthus Aristeguieta

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped. Medium-sized, average longest axis 33μ. Tectate-perforate, columellae reticulate, distinct and well-developed.

Number of species examined: 1 out of 1. Plates: 3:7.

Oxandra A. Rich.

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped. Medium-sized, longest axis 31–48μ, average 39μ. Tectate, columellae random to reticuloid, distinct, somewhat reduced, slightly subsaccate in some grains.

Number of species examined: 10 out of 25. Plates: 3:10–12.

Ruizodendron R. E. Fries

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped, with an oblong-elliptic AMB. Medium-sized, average longest axis 39μ. Tectate, columellae distinct, somewhat reduced, prominently subsaccate.

Number of species examined: 1 out of 1. Plates: 4:7.

Unonopsis R. E. Fries

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped. Large, longest axis 50–87μ, average 69μ. Tectate-perforate, columellae distinct, well-developed, random to highly reticulate.

Number of species examined: 12 out of 33. Plates: 1:2; 5:1–2.

Bocageopsis R. E. Fries

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped. Medium-sized, average longest axis 44μ. Tectate-perforate, columellae distinct, well-developed, random, slightly subsaccate.

Number of species examined: 1 out of 3. Plates: 4:6.

Onychopetalum R. E. Fries

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate, the sulcus long and narrow. Boat-shaped. Medium-sized, longest axis 40–42μ, average 41μ. Tectate, columellae distinct but somewhat reduced, prominently perisaccate with distinctive loose folds.

Number of species examined: 2 out of 4. Plates: 4:1–5.

Enantia Oliv.

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped. Large, average longest axis 64μ. Tectate-perforate, columellae distinct and well-developed, reticulate.

Number of species examined: 1 out of 10. Plates: 5:4–5.

THE UVARIA TRIBE

POLLEN MORPHOLOGY: Pollen grains solitary, rarely in tetrads (*Mitrephora, Pseuduvaria*). Apolar (rarely heteropolar or isopolar), radiosymmetric (rarely bilateral). Inaperturate, rarely sulcate (*Desmos, Friesodielsia, Polyceratocarpus, Uvaria* spp., *Polyalthia* spp., *Artabotrys* spp., *Monocarpia*) or disulculate (*Sapranthus*). Globose to rarely boat-shaped or oblong-elliptic. Medium-sized or large (rarely small), long axis measurement averages for the genera 25–77μ, average for the tribe 45μ. Tectate or

tectate-perforate, columellae distinct (rarely indistinct), well-developed to reduced, random to reticulate, exine surface various—often verrucate, less frequently gemmate, baculate, or strongly echinate *(Desmos, Dasymaschalon,* and *Friesodielsia).* Exine much reduced in *Sapranthus* and *Duguetia,* less so in *Uvaria, Anomianthus, Tetrapetalum,* and *Cyathostemma.*

Mitrephora and *Pseuduvaria* are distinctive with their predominantly tetrahedral tetrads. *Desmos, Dasymaschalon,* and *Friesodielsia* are set apart by their very prominent echinate sculpturing. Although the pollen of *Sapranthus* is disulculate, the genus is closely related to *Stenanona, Reedrollinsia,* and *Desmopsis* and belongs in the *Uvaria* tribe on the basis of the totality of its characters.

Desmos Lour.

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar or apolar, bilateral or radiosymmetric. Sulcate or inaperturate (or possibly sulcate condition difficult to ascertain in the latter). Boat-shaped but more frequently globose, oblong, or elliptical. Medium-sized or large *(D. cochinchinensis),* longest axis 34–60μ, average 45μ. Microtectate, echinate (supratectal ?) with spines up to 4μ long and micromucronate. Exine with minute columellae-like pattern in some species, others with more or less transparent, crystalline exine.

Three of the nine species examined were not echinate and differed from the other species in a number of characters and hence may be misplaced in the genus. They are *D. insularis, D. leucanthus,* and *D. monogynus.*

Number of species examined: 9 out of ca. 25. Plates: 5:8–11; 6:4.

Dasymaschalon (Hk.f. & Th.) Dalla Torre & Harms

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate (if any sulci occur they are difficult to distinguish from folds in the exine). Globose to oblong. Mostly medium-sized, a little larger than 50μ in *D. glaucum,* longest axis 32–54μ, average 41μ. Microtectate, echinate (supratectal ?), with well-developed spines which are micromucronate. Exine with minute columellae-like pattern which is definitely scabrate sculpturing and not infratectal columellae in *D. sootepense.* The pollen of *D. clusiflorum* is distinctive in not being echinate but coarsely verrucate.

Number of species examined: 5 out of ca. 12. Plates: 1:6; 5:12; 6:1–3; 7:1–3; 58:1–2.

Friesodielsia van Steenis (=Oxymitra Bl. ex Hk.f. & Th.)[6]

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar or apolar, bilateral or radiosymmetric. Sulcate (?) or inaperturate (the sulcate condition being difficult to distinguish from chance folds in the rather thin exine), possibly catasulcate in *F. bakeri* (from an apparent dyad). Globose to oblong to oval. Medium-sized, longest axis 35–48μ, average 42μ. Microtectate, echinate (supratectal?) with spines well-developed and micromucronate (somewhat reduced in *F. glauca*). Exine with minute columellae-like pattern or more or less crystalline.

The African species are not congeneric with the Asian genus *Friesodielsia.* cf., ***Friesodielsia*** **(African).**

Number of species examined: 4 out of ca. 40. Plates: 7:4–5.

Monanthotaxis Baill.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 28μ. Microtectate, microbaculate (supratectal ?). Exine with no distinct columellae pattern.

Number of species examined: 1 out of 4. Plates: 6:5.

[6] ***Oxymitra*** **is a later homonym of a genus of hepatics. Both Fries (1959) and Hutchinson (1964) considered** *Oxymitra* **congeneric with the genus** ***Richella*** **(cf., fn. 15, p. 56), but this can no longer be supported, as pollen morphology clearly shows that the two genera belong in separate subfamilies. In 1948 van Steenis proposed a new name,** *Friesodielsia,* **for the genus.**

Enneastemon Exell

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Small to medium-sized, longest axis 23–26μ, average 25μ. Microtectate, microbaculate (supratectal ?). Exine with no distinct columellae pattern.

Number of species examined: 3 out of ca. 10. Plates: 6:6; 7:6.

Popowia Endl. (African)

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, longest axis 29–36μ, average 33μ. Tectate to microtectate, coarsely verrucate to microbaculate. Exine with distinct columellae or transparent and crystalline without discernible columellae.

The species from Africa and Madagascar which have been described under the genus *Popowia* are not congeneric with the Asian *Popowia,* cf., Verdcourt, 1969.

Number of species examined: 3 out of ca. 65. Plates: 15:8–12.

Desmopsis Safford

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized to large, longest axis 30–60μ, average 52μ. (The pollen of *D. stenopetala* is somewhat smaller than the others, averaging 30μ.) Tectate, columellae distinct, somewhat well-developed, random, exine surface pattern low verrucate with verrucate areas appearing as dark, often elongate patches at level when columellae are in focus.

Number of species examined: 11 out of ca. 16. Plates: 7:10; 8:4–5.

Stenanona Standl.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, longest axis 46–50μ, average 48μ. Tectate, columellae random, distinct and well-developed, exine surface pattern loosely verrucate.

Number of species examined: 2 out of 2. Plates: 7:7–8.

Reedrollinsia Walker, gen. nov.[7]

FLORAL MORPHOLOGY: Flowers cauliflorous, peduncle articulate, with a bract both above and below the articulation. Sepals 4–5, in one whorl and basally fused, petals variable in number, mostly in two whorls of 4–5 each, long and strap-shaped, valvate, maroon at maturity. Stamens peltate. Ovules several (ca. 4), lateral.

DISTRIBUTION: The single species is found in the state of Chiapas, Mexico.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 50μ. Tectate, columellae random, distinct and well-developed, exine surface pattern low verrucate with verrucate areas appearing as dark, more or less rounded patches at level when columellae are in focus. Sculpturing more or less psilate with some pits and the exine surface compressed into islands of weakly upraised areas (these appearing as the dark patches in LO-analysis).[8]

Number of species examined: 1 out of 1. Plates 7:9; 8:1–3; 60:1–2.

Sapranthus Seem.

POLLEN MORPHOLOGY: Pollen grains solitary. Isopolar, radiosymmetric or bilateral. Disulculate. Globose or oblong. Medium-sized to large, longest axis 32–62μ, average 52μ (measurements from unacetylated, KOH-treated grains). Tectate, columellae faint but discernible, random to reticulate. Exine thin and quite reduced, intine thick.

Number of species examined: 9 out of ca. 12. Plates: 17:6–7; 18:1–4.

Tetrameranthus R. E. Fries

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate.

[7]Flores cauliflori, pedunculus articulatus, cum bractea et supra et infra articulum. Sepala 4–5, in uno verticillo et basaliter connata, petala quoad numerum variabilia, pro parte maxima in verticillis duobus cum 4–5 petalis uterque, longa et ligulata, valvata, ad maturitatem marronina. Stamina peltata. Pollen inapertum. Ovula aliquot (ca. 4), lateralia. *Walker* 357–GH (holotype); NY, US (isotypes).

This new genus of *Annonaceae* is named after my mentor and friend, Dr. Reed C. Rollins, Asa Gray Professor of Systematic Botany and Director of the Gray Herbarium of Harvard University.

[8]Cf., Erdtman (1966) for a discussion of LO-analysis.

Globose. Medium-sized, average longest axis 44μ. Microtectate, columellae not discernible, exine surface psilate.

Number of species examined: 1 out of 2. Plates: 7:11.

Duguetia St. Hil.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized or large, longest axis 30–80μ, average 49μ (measurements from unacetylated, KOH-treated grains). Tectate, columellae discernible but highly reduced, exine thin and quite reduced.

Number of species examined: 10 out of 74. Plates 7:12.

Polyceratocarpus Engl. & Diels

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate, with a fragile sulcus with ragged margins. Boat-shaped. Large, average longest axis 54μ. Tectate, columellae distinct but somewhat reduced.

Number of species examined: 1 out of 7–8. Plates: 5:6–7.

Uvaria L.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric (rarely heteropolar and bilateral). Inaperturate (rarely sulcate, with the sulcus reduced in length, in *U. bipindensis*). Globose. Medium-sized to large, longest axis 40–82μ, average 57μ. Tectate, columellae discernible to indiscernible, reduced, exine generally thin and reduced, usually with characteristic wrinkled appearance. (Columellae rather well-developed in *U. bipindensis* and distinctly tectate-perforate.)

Number of species examined: 16 out of ca. 175. Plates: 8:6; 9:1–2.

Anomianthus Zoll.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 41μ. Tectate, columellae discernible, reduced, random, exine somewhat reduced.

Number of species examined: 1 out of 1. Plates: 9:3.

Tetrapetalum Miq.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 50μ. Tectate, columellae distinct, random, exine somewhat reduced, with wrinkled appearance.

Number of species examined: 1 out of 2. Plates: 9:4.

Ellipeia Hk.f. & Th.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 32μ. Tectate, columellae distinct, random, exine with somewhat of a wrinkled appearance.

Number of species examined: 1 out of ca. 5. Plates: 9:5.

Cyathostemma Griff.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized or large, longest axis 44–82μ, average 62μ. Tectate, columellae distinct but reduced, exine reduced, with wrinkled appearance.

Number of species examined: 3 out of 8. Plates: 9:6.

Enicosanthum Becc.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, longest axis 40–48μ, average 43μ. Tectate, columellae very well-developed, random to loosely reticuloid. Exine surface weakly verrucate, the verrucate areas more or less irregular and appearing as darker areas at lower focus.

Number of species examined: 3 out of ca. 16. Plates: 9:7–8.

Cleistopholis Pierre ex Engl.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose to oblong. Medium-sized, longest axis 36–48μ, average 42μ. Tectate, columellae distinct but not very strongly developed, random.

Number of species examined: 2 out of 3–4. Plates: 9:9.

Friesodielsia van Steenis (African)

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Large, longest axis 52–56μ, average 54μ. Tectate and coarsely verrucate.

It is evident that the African species described under this genus are not congeneric with the Asian *Friesodielsia.*

Number of species examined: 2 out of ca. 15.

Sageraea Dalzell

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, longest axis 38–40μ, average 39μ. Tectate, columellae very well-developed, random. Exine surface weakly verrucate, the verrucate areas appearing as darker spots at lower focus.

Number of species examined: 3 out of ca. 9. Plates: 9:10; 10:1.

Stelechocarpus (Bl.) Hk.f. & Th.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 26μ. Tectate, columellae distinct, reduced. Exine surface very weakly verrucate, the verrucate areas more or less elongate.

Number of species examined: 1 out of 5. Plates: 9:11.

Alphonsea Hk.f. & Th.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized to large, longest axis 44–82μ, average 53μ. Tectate, columellae distinct, more or less well-developed. Exine surface weakly verrucate to rather well-developed verrucate.

Number of species examined: 10 out of ca. 30. Plates: 9:12; 11:1.

Rauwenhoffia Scheff.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Large, longest axis 66–94μ, average 77μ. Tectate, columellae distinct. Exine surface coarsely verrucate.

Number of species examined: 3 out of 5. Plates: 10:2; 11:2.

Polyalthia Bl.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric (rarely heteropolar and bilateral). Inaperturate (sulcate in *P. glauca* and *P. hypoleuca*). Globose (rarely boat-shaped). Medium-sized to large, longest axis 30–74μ, average 44μ. Tectate, columellae generally distinct, usually well-developed, exine surface verrucate with verrucate areas often appearing as very distinct, more or less irregular, dark patches at lower focus. In the two sulcate species, tectate-perforate, columellae very well-developed, highly reticulate. Sculpturing (in *P. glauca*) psilate with medium-sized perforations in the tectum.

Pollen and floral morphology require the removal of *P. petelotii* and *P. plagioneura* from *Polyalthia* and their transference to the genus *Disepalum* (cf., pollen description for *Disepalum*).

Number of species examined: 22 out of ca. 150. Plates: 10:3–6; 11:3–8; 13:1; 57:5–6.

Meiogyne Miq.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized to large, longest axis 40–56μ, average 49μ. Tectate, columellae distinct to faint, more or less irregular.

Number of species examined: 3 out of ca. 8.

Chieniodendron Tsiang & P.T. Li

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 48μ. Tectate, columellae distinct, more or less irregular.

Number of species examined: 1 out of 1. Plates: 11:9.

Mezzettia Becc.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate.

Globose. Medium-sized, longest axis 30–36μ, average 34μ. Tectate, columellae distinct, random.

Number of species examined: 4 out of 7. Plates: 11:10.

Woodiella Merr.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 32μ. Tectate, columellae distinct, exine surface coarsely verrucate.

Number of species examined: 1 out of 1. Plates: 11:11–12.

Neouvaria Airy-Shaw

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 32μ. Tectate, columellae indistinct, exine surface microbaculate.

Number of species examined: 1 out of 2. Plates: 12:1–2.

Papualthia Diels

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized to large, longest axis 34–60μ, average 48μ. Tectate, columellae well-developed to faint, random, exine surface sometimes verrucate with the verrucate areas prominent as darker, more or less rounded patches at lower focus.

Number of species examined: 5 out of ca. 20. Plates: 12:3; 13:2.

Miliusa Leschen. ex A. DC.
(including Saccopetalum Benn.)

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized or large, longest axis 36–58μ, average 42μ *(Miliusa)* or 51μ *(Saccopetalum)*. Tectate, columellae generally well-developed, exine surface sometimes verrucate with the verrucate areas prominent as darker, more or less rounded patches at lower focus, sometimes distinctly gemmate *(M. campanulata)*.

Number of species examined: 9 out of ca. 40. Plates: 12:4–7; 13:3–4; 12:8.

Fissistigma Griff.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized to large, longest axis 30–56μ, average 41μ. Tectate, columellae distinct, random.

Number of species examined: 7 out of ca. 80. Plates: 12:9.

Mitrella Miq.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 36μ. Tectate, columellae distinct, random.

Number of species examined: 1 out of 5. Plates: 12:10.

Melodorum Lour.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Large, longest axis 64–70μ, average 67μ. Tectate, columellae distinct, somewhat well-developed, random.

Number of species examined: 2 out of ca. 3. Plates: 12:11.

Oncodostigma Diels

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, longest axis 36–42μ, average 39μ. Tectate, columellae distinct, random.

Number of species examined: 2 out of 3. Plates: 12:12.

Guamia Merr.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 40μ. Tectate, columellae distinct, random.

Number of species examined: 1 out of 1. Plates: 14:1–2.

Artabotrys R. Br.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric, sometimes

heteropolar and bilateral. Inaperturate or sulcate with a reduced sulcus (*A. suaveolens, A. trichopetalus*). Globose. Medium-sized to large, longest axis 38–60μ, average 51μ. Tectate, columellae distinct, sometimes well-developed, random, exine surface sometimes weakly verrucate.

Number of species examined: 6 out of ca. 100. Plates: 13:5; 14:3–8.

Monocarpia Miq.

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped. Large, average longest axis 81μ. Tectate-perforate, columellae distinct and well-developed, reticulate.

Number of species examined: 1 out of 1. Plates: 5:3.

Cyathocalyx Champ. ex Hk.f. & Th.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose to oblong-elliptic. Large to medium-sized, longest axis 43–80μ, average 65μ. Tectate-perforate, columellae distinct, random to reticuloid. (*Cyathocalyx suaveolens* differs somewhat and may be sulcoidate.)

Number of species examined: 7 out of ca. 15. Plates: 14:9–10.

Drepananthus Maing. ex Hk.f.

POLLEN MORPHOLOGY: Pollen grains solitary Apolar, radiosymmetric. Inaperturate. Globose. Large to medium-sized, longest axis 47–75μ, average 66μ. Tectate, columellae distinct, random.

Number of species examined: 5 out of ca. 10. Plates: 14:11.

Orophea Bl.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, longest axis 40–50μ, average 45μ. Tectate, columellae distinct, random. (Grains of *O. ellipanthoides* and *O. luzonensis* are in tetrads and are highly verrucate. Their pollen morphology strongly resembles that of *Pseuduvaria* and they may be misplaced in the genus *Orophea*.)

Number of species examined: 9 out of ca. 60. Plates: 14:12; 15:1,7; 16:5; 58:3 -5.

Platymitra Boerl.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 33μ. Tectate, columellae distinct, random.

Number of species examined: 1 out of 2. Plates: 15:2.

Mitrephora Hk.f. & Th.

POLLEN MORPHOLOGY: Pollen grains in tetrahedral tetrads, longest tetrad axis 70–90μ. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized to large, longest axis 44–62μ, average 55μ. Tectate, columellae distinct, random, exine surface sometimes rather well-developed verrucate.

Number of species examined: 7 out of ca. 40. Plates: 13:6; 16:1.

Pseuduvaria Miq.

POLLEN MORPHOLOGY: Pollen grains in tetrahedral tetrads (occasionally tetragonal, rhomboidal, or decussate), longest tetrad axis 50–65μ. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, longest axis 30–38μ, average 35μ. Tectate, columellae distinct, very well-developed, exine surface frequently extremely verrucate with verrucate areas appearing as very distinct dark patches at lower focus. Sculpturing (in *Orophea luzonensis*=? *Pseuduvaria* sp.) extremely well-developed verrucate with small perforations appearing in the tectum at very high magnification.

Number of species examined: 4 out of ca. 35. Plates: 15:3–6; 16:2–4 (see also 15:7; 16:5; 58:3–5).

Popowia Endl.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, longest axis 31–44μ, average 35μ. Tectate, columellae distinct, random, exine surface weakly verrucate.

The African species are not congeneric with the totally Asian genus *Popowia,* cf., *Popowia* (African).

Number of species examined: 4 out of ca. 40.[9] Plates 17:1–2.

Phaeanthus Hk.f. & Th.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized or large, longest axis 46–67μ, average 57μ. Tectate, columellae distinct or faint, random, exine surface more or less smooth, reduced or somewhat weakly verrucate.

Number of species examined: 2 out of ca. 20. Plates: 16:6; 17:3–4.

Trivalvaria Miq.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, longest axis 48–50μ, average 49μ. Tectate, columellae distinct, random.

Number of species examined: 2 out of ca. 6. Plates: 17:5.

THE GUATTERIA TRIBE

POLLEN MORPHOLOGY: Pollen grains solitary. Isopolar, bilateral or radiosymmetric. Disulculate. Elliptic to oblong to rounded. Large, long axis measurement averages for the genera 63–90μ, average for the tribe 74μ (measurements from unacetylated, KOH-treated grains). Microtectate, exine highly reduced, no columellae discernible or possible columellae faint, intine thick.

The members of this tribe have very similar pollen which is distinctive for the family in being disulculate. The only genus outside of this tribe with disulculate pollen is *Sapranthus,* which belongs in the *Uvaria* tribe on the basis of all its characters. The pollen of the *Guatteria* tribe is also notable for its highly reduced exine, which is quite remarkable for a non-aquatic group.

Guatteria Ruiz. & Pav.

POLLEN MORPHOLOGY: Pollen grains solitary. Isopolar, bilateral (and possibly radiosymmetric also). Disulculate. Elliptical and other shapes possibly. Large, average of longest axis 90μ (measurements from unacetylated, KOH-treated grains and a very limited sample). Microtectate, exine highly reduced, faint columellae (?) visible, intine thick.

In some material studied the exine appeared to be almost totally absent. Pollen grains of *G. anomala* (subgenus *Anomalantha*) had an extremely reduced exine.

Number of species examined: 1 out of ca. 250.[10] Plates: 17:8; 18:5–6.

Guatteriopsis R. E. Fries

POLLEN MORPHOLOGY: Pollen grains solitary. Isopolar, radiosymmetric. Disulculate. Globose. Large, average longest axis 70μ (measurements from unacetylated, KOH-treated grains). Microtectate, exine highly reduced, no columellae discernible, intine thick.

Number of species examined: 1 out of 4. Plates: 17:9.

Heteropetalum Benth.

POLLEN MORPHOLOGY: Pollen grains solitary. Isopolar, bilateral. Disulculate. Elliptical-

[9]A duplicate sheet of a type collection cited by Diels as *Popowia pachypetala* found in the herbarium of the Arnold Arboretum has tricolpate pollen and is not material of the family *Annonaceae.*

[10]Permanent slides were prepared for only one species of this genus, which is palynologically difficult to prepare; however, non-permanent slides were made of about a dozen species, including both subgenera.

oblong. Large, average of longest axis 63μ (measurements from unacetylated, KOH-treated grains). Microtectate, exine highly reduced, no columellae discernible, intine thick.

Number of species examined: 1 out of 2. Plates: 17:10–12.

THE FUSAEA SUBFAMILY

POLLEN MORPHOLOGY: Pollen grains solitary *(Anaxagorea, Piptostigma)*, in tetragonal tetrads or polyads of ca. 5–6 usually individually discernible tetrads *(Xylopia)*, or in very loose tetragonal to tetrahedral tetrads. Stamens septate with each tetrad or polyad in a separate compartment in *Xylopia, Neostenanthera, Goniothalamus,* and *Richella.* Heteropolar, bilateral. Sulcate *(Anaxagorea, Piptostigma)* or catasulcate to cataulcerate. Boat-shaped, more or less globose, triangular, or disc-like, concave-convex. Large to very large, long axis measurement averages for the genera 67–141μ, average for the subfamily 92μ. Microtectate, columellae (?) faint, mostly not discernible, exine surface more or less psilate, often with conspicuous pitting.

The *Fusaea* subfamily is notable because the pollen grains of all its members (except *Anaxagorea* and *Piptostigma*) are in tetrads or polyads (*Xylopia* spp.). The occurrence of septate stamens in *Xylopia, Neostenanthera, Goniothalamus,* and *Richella* is also noteworthy. Pollen gigantism is present in a number of species in this subfamily, which is characterized by the extreme reduction of the columellae so that they are indiscernible, and by the very thick and more or less psilate exine.

Anaxagorea St. Hil.

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped to more or less globose. Large, longest axis 56–95μ, average 70μ. Microtectate, columellae (?) faint to more or less indiscernible, exine somewhat reduced, exine surface more or less psilate.

Number of species examined: 11 out of 29. Plates: 19:1–8; 20:1–2; 21:1–2.

Piptostigma Oliv.

POLLEN MORPHOLOGY: Pollen grains solitary. Heteropolar, bilateral. Sulcate. Boat-shaped. Large, longest axis 57–76μ, average 67μ. Microtectate, columellae (?) faint but discernible, exine somewhat reduced, exine surface more or less psilate.

Number of species examined: 3 out of 15. Plates: 22:1–3.

Xylopia L.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads or polyads of ca. 5–6 usually individually discernible tetrads *(X. brasiliensis, X. ferruginea, X. micans, X. africana)*. Stamens septate with each tetrad or polyad in a separate compartment. Heteropolar, bilateral. Catasulcate to cataulcerate. Boat-shaped to triangular to disc-like. Large to very large, longest axis 52–170μ, average 87μ. Microtectate, columellae (?) present, exine somewhat reduced to well-developed, more or less psilate, often with conspicuous pitting.

Number of species examined: 15 out of ca. 170. Plates: 22:4–8; 23:1–6; 24:1–5; 25:1–2.

Fusaea (Baill.) Saff.

POLLEN MORPHOLOGY: Pollen grains in very loose tetragonal to tetrahedral tetrads. Heteropolar, bilateral. Cataulcerate. Disc-like, concave-convex. Very large, longest axis 103–126μ, average 115μ. Microtectate, no columellae discernible, exine very

thick, exine surface with pitting, otherwise psilate. Sculpturing (in *F. longifolia*) psilate, with infrequent pits, Übisch bodies very conspicuous.

Number of species examined: 2 out of 3. Plates: 22:9; 26:1; 27:1; 59:4–5.

Duckeanthus R. E. Fries

POLLEN MORPHOLOGY: Pollen grains in very loose tetragonal to tetrahedral tetrads. Heteropolar, bilateral. Cataulcerate. Disc-like, concave-convex. Very large, average longest axis 141μ. Microtectate, no columellae discernible, exine very thick, psilate.

Number of species examined: 1 out of 1. Plates: 26:2; 27:2.

Cananga Hk.f. & Th.

POLLEN MORPHOLOGY: Pollen grains in very loose tetragonal to tetrahedral tetrads. Heteropolar, bilateral. Cataulcerate. Boat-shaped-oblong to rounded. Large to very large, longest axis 96–107μ, average 102μ. Microtectate, columellae (?) present, pitting very conspicuous, especially in *C. latifolia*. Aperture margin conspicuously subsaccate in *C. odorata*, giving a very wrinkled appearance to the proximal face of the grains. Sculpturing (in *C. odorata*) psilate, with some pits, Übisch bodies conspicuous.

Number of species examined: 2 out of 2. Plates: 22:10; 26:3–6; 27:3–6; 59:1–2.

Meiocarpidium Engl. & Diels

POLLEN MORPHOLOGY: Pollen grains in very loose tetragonal to tetrahedral tetrads. Heteropolar, bilateral. Cataulcerate. Disc-like, concave-convex. Large, average longest axis 96μ. Microtectate, no columellae discernible, exine thick, exine surface pitted, otherwise more or less psilate.

Number of species examined: 1 out of 1. Plates: 28:1.

Neostenanthera Exell

POLLEN MORPHOLOGY: Pollen grains in very loose tetragonal to tetrahedral tetrads. Stamens septate, with each tetrad probably in a separate compartment. Heteropolar, bilateral. Cataulcerate. Disc-like, concave-convex. Large, longest axis 65–81μ, average 73μ. Microtectate, no columellae (?) discernible, exine surface pitted, otherwise psilate.

Number of species examined: 3 out of ca. 6. Plates: 22:11–12; 29:1.

Goniothalamus (Bl.) Hk.f. & Th.

POLLEN MORPHOLOGY: Pollen grains in very loose tetrahedral to tetragonal tetrads. Stamens septate, with each tetrad in a separate compartment. Heteropolar, bilateral. Cataulcerate. Disc-like, concave-convex. Large, very large in *G. curtisii* (up to 140μ), longest axis 71–140μ, average 95μ. Microtectate, no columellae discernible, exine surface often pitted, otherwise psilate.

Number of species examined: 9 out of ca. 80. Plates: 28:2–5; 29:2–4; 30:1–3.

Richella A. Gray

POLLEN MORPHOLOGY: Pollen grains in very loose tetrahedral to tetragonal tetrads. Stamens septate, with each tetrad in a separate compartment. Heteropolar, bilateral. Cataulcerate. Disc-like, concave-convex. Large, average longest axis 71μ. Microtectate, no columellae discernible, exine surface with some pits, otherwise psilate.

Number of species examined: 1 out of 1–2. Plates: 29:5; 30:4.

THE ANNONA SUBFAMILY

POLLEN MORPHOLOGY: Pollen grains in tetrads or polyads (*Cymbopetalum* tribe), rarely solitary (*Isolona* and *Cleistochlamys* of the *Hexalobus* tribe and a few *Annona* spp., *Rollinia*, and *Rolliniopsis* in the *Annona* tribe). Heteropolar (or apolar), bilateral (or radiosymmetric). Catasulcate to cataulcerate, rarely inaperturate (*Isolona*, *Cleistochlamys*, *Annona* spp.,

Rollinia, and *Rolliniopsis*). Boat-shaped-triangular, rounded, oblong, elliptic, or globose. Medium-sized to gigantic (rarely small—*Cleistochlamys*), long axis measurement averages for the genera 24–183μ, average for the subfamily 83μ (extreme length up to 350μ in *Cymbopetalum odoratissimum*). Tectate-perforate to tectate, rarely intectate (in *Trigynaea* of the *Cymbopetalum* tribe), perforations sometimes very large, up to 15μ, columellae usually extremely well-developed to reduced, random to reticulate to ornate. Exine often very thick, up to 20μ thick in the *Cymbopetalum* tribe and more or less entirely wanting on the inner face of many members of this subfamily.

This subfamily is notable because the pollen of the great majority of its members is either in tetrads or polyads (the *Cymbopetalum* tribe). The *Cymbopetalum* tribe is very remarkable for its almost constantly septate stamens with each polyad being in a separate compartment, for its pollen gigantism (up to 350μ), and for the almost total lack of exine on the proximal face of the grains. The genus *Trigynaea* of the *Cymbopetalum* tribe is the only genus in the family which is definitely intectate. The subfamily is characterized by the extremely well-developed columellae which reach their peak in the *Cymbopetalum* tribe.

THE HEXALOBUS TRIBE

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads or solitary (*Isolona*, *Cleistochlamys*). Heteropolar (or apolar), bilateral (or radiosymmetric). Catasulcate to cataulcerate (inaperturate in *Isolona* and *Cleistochlamys*). Boat-shaped-triangular or globose. Large (rarely medium-sized or small—*Cleistochlamys*), long axis measurement averages for the genera 24–93μ, average for the tribe 60μ. Tectate-perforate or tectate, columellae distinct, random to reticulate.

Diclinanona stands apart from the other genera in this group both phytogeographically and with respect to its floral morphology.

Monodora Dunal

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate (some cataulceroidate?). Boat-shaped to more or less triangular. Large (medium-sized at 30μ in *M. angolensis*), longest axis 30–86μ, average 65μ. Tectate, some perforations present but not very prominent, columellae distinct, random.

Number of species examined: 5 out of ca. 20. Plates: 28:6; 31:1.

Isolona Engl.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Large, longest axis 52–65μ, average 58μ. Tectate, columellae distinct, random.

Number of species examined: 4 out of ca. 20. Plates: 29:6–8.

Uvariastrum Engl.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Boat-shaped-triangular. Large, longest axis 55–68μ, average 62μ. Tectate-perforate, columellae distinct, random.

Number of species examined: 3 out of ca. 7. Plates: 29:9–12; 31:2.

Uvariopsis Engl.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Boat-shaped-triangular. Large, longest axis 50–62μ, average 56μ. Tectate-perforate, columellae distinct (very well-developed in *U. guineensis*), random.

Number of species examined: 2 out of ca. 13. Plates: 31:3; 32:1–3.

Hexalobus A. DC.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Boat-shaped-triangular. Large, average longest axis 60μ. Tectate-perforate, columellae very well-developed, reticulate.

Number of species examined: 1 out of 5. Plates: 31:4–6; 32:4–5.

Cleistochlamys Oliv.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Small, average longest axis 24μ. Tectate, columellae distinct, well-developed, especially relative to grain size, some fused laterally into arcs, more or less random.

Number of species examined: 1 out of 1. Plates: 32:6–9.

Diclinanona Diels

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Boat-shaped-triangular. Large, average longest axis 93μ. Tectate-perforate, columellae distinct, very well-developed, some fused laterally into arcs, etc., random.

Number of species examined: 1 out of 2. Plates: 30:5; 32:10–11.

THE ASIMINA TRIBE

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Boat-shaped-triangular to oblong to rounded. Very large to large, long axis measurement averages for the genera 97–104μ, average for the tribe 101μ. Tectate-perforate, perforations prominent, more or less circular to elongate to slit-like, up to 4–5μ in *Asimina* and up to 9–12μ in *Deeringothamnus*, columellae very well-developed, solitary or fused laterally, random to reticulate.

Deeringothamnus with its strongly rounded grains with large, more or less circular perforations up to 12μ, and the strongly reticulate pattern of its columellae, is palynologically quite distinct from *Asimina*.

Asimina Adans.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads, longest tetrad axis 120–180μ. Heteropolar, bilateral. Catasulcate to cataulcerate. Shape varied, from boat-shaped-triangular to oblong to rounded. Very large to large, longest axis 84–114μ, average 104μ. Tectate-perforate, perforations prominent, up to 4–5μ, more or less circular to elongate to slit-like, columellae very well-developed, solitary to fused laterally into arcs and various ornate patterns, more or less random to reticuloid, moderately packed to tightly packed.

Number of species examined: 8 out of 8. Plates: 30:6; 33:1–4; 34:1–6; 35:1–5; 37:3.

Deeringothamnus Small

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Cataulcerate. Oblong to rounded. Large to very large, longest axis 90–103μ, average 97μ. Tectate-perforate, perforations mostly circular, some elongate, very large–up to 9–12μ, columellae very well-developed, mostly solitary, a few fused laterally into arcs, etc., reticulate.

Number of species examined: 2 out of 2. Plates: 35:6; 36:1–6; 37:1–2.

THE ANNONA TRIBE

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads to solitary (a few *Annona* spp., *Rollinia, Rolliniopsis*). Heteropolar or apolar, bilateral or radiosymmetric. Catasulcate, cataulcerate, or inaperturate (a few *Annona* spp., *Rollinia, Rolliniopsis*). Oblong, elliptic, rounded, or globose. Gigantic to medium-sized, long axis measurement averages for the genera 49–107μ, average for the tribe 68μ. Tectate-perforate to tectate, columellae well-developed to faint, random to reticulate or ornate.

The genus *Raimondia* (exclusive of *R. tenuiflora*) is palynologically somewhat distinct within the tribe, especially with regard to its prominent tectal perforations.

The solitary grains found in *Rollinia, Rolliniopsis,* and the more advanced, West Indian species of *Annona* are clearly secondary and derived from grains which were in tetrads. This is a noteworthy reversal of the normal trend from solitary grains to tetrads.

Annona L.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads to rarely solitary. Heteropolar or apolar, bilateral or radiosymmetric. Catasulcate, cataulcerate, cataulceroidate, or inaperturate. Oblong, elliptic, rounded, or globose. Gigantic to medium-sized, longest axis 30–283μ, average 107μ. Tectate-perforate to tectate, perforations large to small, circular to elongate, columellae well-developed to faint, solitary, fused laterally in 2's or 3's, reticulate or highly ornate, loosely packed to tightly packed.

Number of species examined: 50 out of ca. 125. Plates: 33:5–12; 37:4–5; 38:1–6; 39:1–6; 40:1–6; 41:1–6; 42:1–6; 43:1–12.

Sect. 1. Annona

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads, longest tetrad axis 200μ to more than 300μ. Heteropolar, bilateral. Catasulcate to cataulcerate. Oblong to elliptic to rounded. Very large to gigantic, long axis measurement averages for the species 135–221μ, average for the section 179μ. Tectate-perforate, perforations more or less circular, some elongate, minute to large, columellae very well-developed, solitary or occasionally a few fused laterally into arcs, etc., medium-packed, random to more or less reticulate.

Number of species examined: 4 out of 17. Plates: 33:5; 38:1–2; 39:1–3.

Sect. 2. Macrantha R. E. Fries

This section, with 3 species, is endemic to South America. No species were examined.

Sect. 3. Ulocarpus Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Oblong to rounded. Very large to gigantic, long axis measurement averages for the species 142–237μ, average for the section 190μ. Tectate-perforate, perforations mostly circular to slightly elongate, columellae very well-developed, solitary to occasionally fused laterally, tightly packed, random to loosely reticulate.

Number of species examined: 2 out of 2. Plates: 39:4.

Sect. 4. Campicola R. E. Fries

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong. Very large, average longest grain axis for the section 159μ. Tectate-perforate, perforations relatively small, usually less than the diameter of the columellae, columellae well-developed, mostly solitary, medium-packed, more or less random to loosely reticulate.

Number of species examined: 1 out of 2. Plates: 38:3; 39:5–6.

Sect. 5. **Psammogenia** Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong. Gigantic, average longest grain axis for the section 283μ. Tectate-perforate, columellae well-developed, mostly solitary, medium-packed, more or less random.

Number of species examined: 1 out of 3.

Sect. 6. **Phelloxylon** Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong. Very large, average longest grain axis for the section 111μ. Tectate-perforate, perforations rather small, more or less circular, columellae well-developed, highly ornate, solitary columellae occasional only.

Number of species examined: 1 out of 1. Plates: 40:1–4.

Sect. 7. **Helogenia** Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong. Medium-sized to large to very large, long axis measurement averages for the species 49–141μ, average for the section 89μ. Tectate to tectate-perforate, perforations small, columellae well-developed, solitary to a few fused laterally, random to highly reticulate.

Number of species examined: 4 out of 9. Plates: 33:6–7; 41:1–3.

Sect. 8. **Pilannona** Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate (cataulceroidate to inaperturate in *A. jamaicensis*). Rounded to oblong to globose (*A. jamaicensis*). Very large, long axis measurement averages for the species 102–156μ, average for the section 120μ (medium-sized in *A. jamaicensis*, average longest grain axis 37μ). Tectate to tectate-perforate, perforations small, mostly circular, columellae well-developed, solitary to fused into arcs to ornate, random to loosely reticulate. *Annona jamaicensis* is quite isolated palynologically from the other species of the section in aperture type, grain shape, and size.

Number of species examined: 9 out of 24. Plates: 33:8; 37:4–5; 40:5–6.

Sect. 9. **Gamopetalum** Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong. Very large, long axis measurement averages for the species 116–118μ, average for the section 117μ. Tectate-perforate, perforations small, columellae well-developed, very tightly packed, solitary to fused laterally into ornate patterns, random to somewhat ornate.

Number of species examined: 2 out of 7. Plates: 38:4; 41:4.

Sect. 10. **Oligantha** R. E. Fries

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong-elliptic. Medium-sized to large, long axis measurement averages for the species 40–79μ, average for the section 60μ. Tectate, columellae well-developed, numerous, more or less random, mostly solitary.

Number of species examined: 2 out of 10–11. Plates: none (but see pl. 44:10, *Raimondia tenuiflora*, which palynologically looks like a member of this section).

Sect. 11. **Atractanthus** Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong. Medium-sized to large, long axis measurement averages for the species 40–64μ, average for the section 53μ. Tectate, columellae well-developed, reticulate.

Number of species examined: 3 out of 5. Plates: 33:9–12; 41:5; 42:1–4.

Sect. 12. **Atta** Mart.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate to cataulceroidate. Rounded to oblong. Medium-sized to large, long axis measurement averages for the species 32–74μ, average for the section 57μ. Tectate, columellae well-developed, random to loosely reticuloid.

Number of species examined: 7 out of 12. Plates: 38:5; 41:6; 42:5–6; 43:1.

Sect. 13. **Chelonocarpus** Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong. Large to very large, long axis measurement averages for the species 91–101μ, average for the section 96μ. Tectate-perforate, columellae well-developed, solitary to ornate to reticulate.

Number of species examined: 2 out of 4. Plates: 38:6; 43:2–3.

Sect. 14. **Ilama** Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong. Large, long axis measurement averages for the species 72–76μ, average for the section 74μ. Tectate, columellae mostly random, mainly solitary.

Number of species examined: 2 out of 2. Plates: 43:4–5.

Sect. 15. **Saxigena** Saff.

POLLEN MORPHOLOGY: Pollen grains in very loose tetragonal tetrads to solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, long axis measurement averages for the species 30–32μ, average for the section 31μ. Tectate, columellae reduced, random.

Number of species examined: 2 out of 2. Plates: 43:6–7.

Sect. 16. **Annonula** Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads or solitary. Heteropolar to apolar, bilateral to radiosymmetric. Cataulcerate to cataulceroidate to inaperturate. Globose to oblong. Medium-sized, long axis measurement averages for the species 34–48μ, average for the section 43μ. Tectate, columellae reduced, random.

Number of species examined: 4 out of 11. Plates: 43:8.

Sect. 17. **Annonella** Baill.

POLLEN MORPHOLOGY: Pollen grains solitary (rarely in loose tetrads). Heteropolar to apolar, bilateral to radiosymmetric. Cataulceroidate to inaperturate. Globose to oblong. Medium-sized to large, long axis measurement averages for the species 42–53μ, average for the section 47μ. Tectate, columellae distinct, random to somewhat reticulate.

Number of species examined: 4 out of 5. Plates: 43:9–12.

Rollinia St. Hil.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized to large, longest axis 35–62μ, average 49μ. Tectate, columellae distinct, random to somewhat reticulate.

Number of species examined: 7 out of ca. 65. Plates: 44:1–6; 45:1–4.

Rolliniopsis Saff.

POLLEN MORPHOLOGY: Pollen grains solitary. Apolar, radiosymmetric. Inaperturate. Globose. Medium-sized, average longest axis 50μ. Tectate, columellae distinct, random.

Number of species examined: 1 out of 4. Plates: 44:7; 45:5.

Raimondia Saff.

POLLEN MORPHOLOGY: Pollen grains in tetragonal tetrads. Heteropolar, bilateral. Catasulcate to cataulcerate. Rounded to oblong. Large, longest axis 52–84μ, average 67μ. Tectate-perforate, perforations large, circular to very elongate, columellae very well-developed, reticulate. (In *R. tenuiflora*, tectate, no large, visible perforations, columellae much smaller, random.) The exine structure of *R. tenuiflora* is unlike the other three species and Fries is probably correct in transferring this species back to *Annona* (section *Oligantha*), with which it is palynologically more harmonious (cf., *Annona* section *Oligantha*).

Number of species examined: 4 out of 4. Plates: 44:8–10; 45:6; 46:1.

THE CYMBOPETALUM TRIBE

POLLEN MORPHOLOGY: Pollen grains in polyads (octads in *Cymbopetalum, Cardiopetalum, Trigynaea,* and *Disepalum;* 16's in *Hornschuchia;* and 16's, 18's, 20's, 24's, etc. in *Porcelia*). Stamens transversely septate at maturity with each polyad in a separate compartment (except in *Disepalum*). Heteropolar, bilateral. Cataulcerate. Rounded to oblong. Large to gigantic, long axis measurement averages for the genera 64–183μ, average for the tribe 104μ. Tectate-perforate or intectate *(Trigynaea),* perforations sometimes very large, up to 15μ, columellae extremely well-developed, random to reticulate, exine very well-developed, often more than 20μ thick, more or less entirely wanting on the inner face.

This tribe is very distinctive in that its pollen always occurs in polyads and all its members except *Disepalum* have septate stamens at maturity, with each polyad in a separate compartment. This group is remarkable for its very large pollen (up to 350μ in *Cymbopetalum odoratissimum*), which is more or less devoid of exine on the proximal face. *Trigynaea* is the only genus in the family definitely with intectate grains (clavate or baculate). *Disepalum* stands somewhat apart within the tribe in being the only non-American genus, in lacking transversely locellate stamens at maturity, in having a single, basal ovule, and in its bracteate peduncle.

Cymbopetalum Benth.

POLLEN MORPHOLOGY: Pollen grains in polyads (octads). Stamens transversely septate with each polyad in a separate compartment. Heteropolar, bilateral. Cataulcerate (sometimes more or less catasulcate). Rounded to oblong. Very large to gigantic, longest axis 130–283μ, average 183μ (some grains in *C. odoratissimum* up to 350μ). Tectate-perforate, perforations sometimes very large, up to 15μ, columellae extremely well-developed, in arcs or solitary, random to reticulate, exine very well-developed, often more than 20μ thick, frequently entirely wanting on inner face, intine thick and escaping (in liquid medium) as a crystalline sphere upon separation of the grains of a polyad. Sculpturing (in *C. odoratissimum*) consisting of a smooth tectum with very large, more or less rounded to elongate to irregular perforations, nexine surface on the proximal face wrinkled, rough.

Number of species examined: 10 out of ca. 13. Plates: 46:2–5; 47:1–6; 48:1–5; 49:1–2: 59:3; 60:3–5; 61:1–2.

Cardiopetalum Schlecht.

POLLEN MORPHOLOGY: Pollen grains in polyads (octads). Stamens transversely septate with each polyad in a separate compartment. Heteropolar, bilateral. Cataulcerate. Rounded to more or less oblong. Very large, average longest axis 108μ. Tectate-perforate, perforations more or less circular, medium-sized to small, columellae very well-developed, mostly solitary, reticulate, exine well-developed, more or less wanting on inner face.

Number of species examined: 1 out of 1. Plates: 46:6; 48:6; 50:1–2.

Porcelia Ruiz & Pav.

POLLEN MORPHOLOGY: Pollen grains in polyads (16's, 18's, 20's, 24's, etc.). Stamens transversely septate with each polyad in a separate compartment. Heteropolar, bilateral. Cataulcerate. Rounded to more or less oblong. Large to very large, longest axis 68–125μ, average 90μ. Tectate-perforate, perforations mostly circular, medium-sized to small, columellae well-developed, mostly solitary, somewhat reticulate, exine well-developed, more or less wanting on inner face.

Number of species examined: 4 out of 5. Plates: 44:11; 49:3–5; 50:3–4.

Trigynaea Schlecht.

POLLEN MORPHOLOGY: Pollen grains in polyads (octads). Stamens transversely septate with each polyad in a separate compartment. Heteropolar, bilateral. Cataulcerate. Rounded. Large, longest axis 56–71μ, average 64μ. Intectate, baculate *(T. caudata, T. ecuadorensis)* or clavate *(T. oblongifolia)*. Exine well-developed, more or less wanting on inner face.

Number of species examined: 3 out of 5. Plates: 44:12; 49:6; 50:5–6; 51:1; 52:1–2; 53:1–2.

Hornschuchia Nees von Esenbech

POLLEN MORPHOLOGY: Pollen grains in polyads (16's). Stamens transversely septate with each polyad in a separate compartment. Heteropolar, bilateral. Cataulcerate. Rounded. Large, average longest axis 84μ. Tectate-perforate, perforations rounded to somewhat elongate-irregular, columellae well-developed, mostly solitary, reticulate, exine well-developed, more or less wanting on inner face.

Number of species examined: 1 out of 3. Plates: 52:3; 53:3.

Disepalum Hk.f.

POLLEN MORPHOLOGY: Pollen grains in polyads (octads). Heteropolar, bilateral. Cataulcerate. Rounded to oblong. Large to very large, longest axis 68–127μ, average 96μ. Tectate-perforate, perforations medium to small (very large in *D. anomalum*), rounded to shortly elongate, columellae well-developed, solitary to fused laterally into arcs, random to reticulate, exine well-developed, more or less wanting on inner face.

Number of species examined: 5 out of ca. 8. Plates: 51:2–6; 52:4–7; 53:4–6; 54:1–6.

Critique of Recent Palynological Studies

As mentioned earlier, the only recent, extensive survey of the pollen of the *Annonaceae* is that of Canright (1963). His study includes pollen from 186 species in 71 genera and was based upon acetylated grains.

The present study has brought to light certain differences with the observations and/or conclusions made by Canright. He states that only 11 genera were found with tetrads, while in the present study some 20 genera were found to be characterized by tetrads, many of which were undoubtedly included in his study. No mention is made in Canright's paper of polyads, while in the present study six genera were found consistently with polyads and a seventh *(Xylopia)* was found to have either tetrads or polyads, depending on the species. *Disepalum* is listed by Canright among the genera with tetrads, while all species of this genus examined in the present study were found to have polyads (octads). *Fissistigma* is listed among the genera with tetrads by Canright, while all examined species were found to have solitary grains in the author's study. Also, he lists *Cremastosperma* among the genera with tetrads. All nine species examined in the present study were found to have solitary grains. A very few rare tetrads (or possibly only chance tetrad-like aggregates) were found in some slides of *C. cauliflorum* (pictured by Canright), but, in my opinion, to list a genus as having tetrads when they may only occur rarely in one species is somewhat misleading.

The tetrads that Canright found were tetragonal or rhomboidal, but not tetrahedral. From the present study the fact emerges that *Pseuduvaria*, *Mitrephora*, and *Pseudoxandra* are characterized by tetrahedral tetrads, even though the majority of the annonaceous tetrads are of the tetragonal type. Canright states that all examined species were characterized by

either a monosulcate or inaperturate condition. However, I have found disulculate pollen in *Guatteria, Guatteriopsis, Heteropetalum,* and *Sapranthus.* The occurrence of disulculate pollen in *Guatteria* is statistically significant for the family at the species level since *Guatteria* is the largest genus with some 250 species. The discovery of disulculate pollen in the family also negates Canright's position relative to the relationship of the *Eupomatiaceae* to the *Annonaceae.*

Canright lists *Cymbopetalum* among genera having the smallest grains in the family (around 20μ), when in actuality this genus probably has the largest, fixiform pollen in the angiosperms with an average of the longest grain axis for the genus of 183μ and a range of averages for the species from 130–283μ (based upon a study of 10 species out of a total of 13 for the genus). He describes the pollen of *Cyathocalyx* and *Drepananthus* as monosulcate although all species of these two genera examined by the author were found to be inaperturate.

Finally, Canright lists *Monodora* as having coherent, inaperturate tetrads and *Isolona* as having solitary, monosulcate grains. The species of the two genera examined in the present study showed *Monodora* to have monosulcate grains in tetrads, while the grains of *Isolona* were found to be solitary and inaperturate. He additionally concludes that *Monodora* and *Isolona* are not closely related, based upon palynological data. This is not borne out by the present study, since a number of examples were found in which one genus of a closely related pair had monosulcate tetrads, while the pollen in the second genus was reduced to solitary, inaperturate grains, e.g., *Hexalobus* and *Cleistochlamys; Annona* and *Rollinia.*

Major Trends of Pollen Evolution

The most important phylogenetic character of pollen morphology is the type of aperture, while polarity, symmetry, and shape are all more or less dependent upon the aperture type. The pollen-unit and exine structure and sculpturing are also of great phylogenetic significance.

Palynologically the *Annonaceae* may be divided into a number of rather distinct groups based primarily upon the type of aperture (table 6). For the most part these groups (based primarily on pollen morphology) are much more natural than the previously recognized infrafamilial groups (based entirely upon floral morphology).

An outline of aperture evolution within the family has been given (table 3) and is reviewed in plate 55. It must be emphasized that plate 55 is only a chart of pollen trends and should not be interpreted as a phylogenetic diagram. The primitive aperture type for the family is clearly the anasulcate grain, which is so common in many of the other "ranalean" families, especially in the closely related *Magnoliaceae* (Canright, 1953) and *Canellaceae* (Wilson, 1964).

Two species of the genus *Pseudoxandra* appear to be the only members

TABLE 6. PALYNOLOGICAL CLASSIFICATION OF THE ANNONACEAE

I. SULCATES, ECHINATES, INAPERTURATES, AND DISULCULATES

A. SULCATES

Anasulcates: Pseudoxandra (some catasulcate).

Catasulcates: Cremastosperma, Malmea, Ephedranthus, Pseudephedranthus, Oxandra, Ruizodendron, Unonopsis, Bocageopsis, Onychopetalum, Enantia, Polyceratocarpus, Uvaria (a few sulcate), Polyalthia (a few sulcate), Artabotrys (a few sulcate), Monocarpia.

B. ECHINATES: Monanthotaxis, Enneastemon, Popowia (African), Desmos, Dasymaschalon, Friesodielsia.

C. INAPERTURATES: Desmopsis, Stenanona, Reedrollinsia, Tetrameranthus, Duguetia, Cleistopholis, Friesodielsia (African), Uvaria (a few sulcate), Anomianthus, Tetrapetalum, Ellipeia, Cyathostemma, Rauwenhoffia, Enicosanthum, Sageraea, Stelechocarpus, Trivalvaria, Polyalthia (a few sulcate), Mezzettia, Chieniodendron, Artabotrys (a few sulcate), Cyathocalyx, Drepananthus, Meiogyne, Oncodostigma, Guamia, Papualthia, Woodiella, Fissistigma, Mitrella, Melodorum, Alphonsea, Miliusa, Saccopetalum, Phaeanthus, Orophea, Platymitra, Mitrephora, Pseuduvaria, Popowia, Neouvaria.

D. DISULCULATES: Sapranthus, Guatteria, Guatteriopsis, Heteropetalum.

II. CATAULCERATES

A. FUSAEA-TYPE CATAULCERATES: Anaxagorea, Piptostigma, Neostenanthera, Xylopia, Duckeanthus, Fusaea, Meiocarpidium, Cananga, Goniothalamus, Richella.

B. ANNONA-TYPE CATAULCERATES

Hexalobus Group: Uvariastrum, Uvariopsis, Cleistochlamys, Hexalobus, Monodora, Isolona, Diclinanona.

Asimina Group: Asimina, Deeringothamnus.

Annona Group: Annona, Raimondia, Rollinia, Rolliniopsis.

Cymbopetalum Group: Cymbopetalum, Cardiopetalum, Porcelia, Trigynaea, Hornschuchia, Disepalum.

of the family to have retained the distally oriented sulcus. Other species of this genus show the transition from anasulcate to catasulcate and it is probably best to consider the other closely related genera such as *Malmea, Cremastosperma, Unonopsis, et al.* as catasulcate also, although future cytological studies may show them to be anasulcate. If the *Malmea* sulcates should prove to be anasulcate, then the majority of the inaperturates (and all the disulculates) would be derived directly from an anasulcate, rather than a catasulcate ancestry.

From this basal group of catasulcates a number of radiations occurred (pl. 55). In one line the sulcus was lost and the grains became inaperturate. Through parallel evolution from two separate inaperturate groups disulculate grains developed. In both groups this type of aperture is correlated with a highly reduced exine. Two other groups developed highly distinctive echinate or microbaculate pollen, the first (*Desmos* and its allies) retaining a sulcus in some members, the second (*Monanthotaxis* and its allies) being inaperturate.

From the basal catasulcate group of genera with moderately well-developed columellae two other parallel but quite distinct lines emerged. They are both characterized by trends toward pollen gigantism, toward the production of tetrads and polyads, toward the formation within the stamens of sterile septa enclosing each tetrad or polyad in a separate

compartment, and toward the formation of a cataulcus rather than an elongate sulcus.

These two lines, however, exhibit two opposite trends relative to the columellae and the surface of the tectum. In the one group, the *Fusaea*-type cataulcerates, the columellae are so highly reduced as to be indiscernible, while in the other, the *Annona*-type cataulcerates, the columellae are enlarged to gigantic dimensions (sometimes up to 10μ wide). Finally, the medium-sized tectal perforations of *Malmea-Cremastosperma* are tremendously enlarged in the *Annona* group (up to 15μ), while they become highly reduced in the *Fusaea* group. The *Annona* and *Fusaea* groups both exhibit a strong trend toward more and more loss of the exine on the inner face of the grain, until the exine is more or less entirely lacking on the proximal side in some genera, e.g., *Cymbopetalum*.

Interestingly enough, the sculpturing trends quite closely parallel the trends in apertures, pollen-units, and exine structure (the columellae). Plate 56, which is made up of a series of scanning electronmicrographs, shows the four major sculpturing trends. The moderate-sized perforations in the tectum of such genera as *Malmea* and *Cremastosperma* (pl. 56:1a) are considered basic for the family. One line continues this pattern (pl. 56:1b). A second line shows the loss of most of the tectal perforations, with the tectum becoming subverrucate (pl. 56:2a) to strongly verrucate (pl. 56:2b) to echinate (pl. 56:2c). A third line, which characterizes the *Fusaea*-type cataulcerates, exhibits a reduction in the perforations (pl. 56:3a) and finally an almost total lack of them (pl. 56:3b and 3c). The fourth line, which characterizes the *Annona*-type cataulcerates, exhibits a great elaboration of the perforations in the tectum (pl. 56:4).

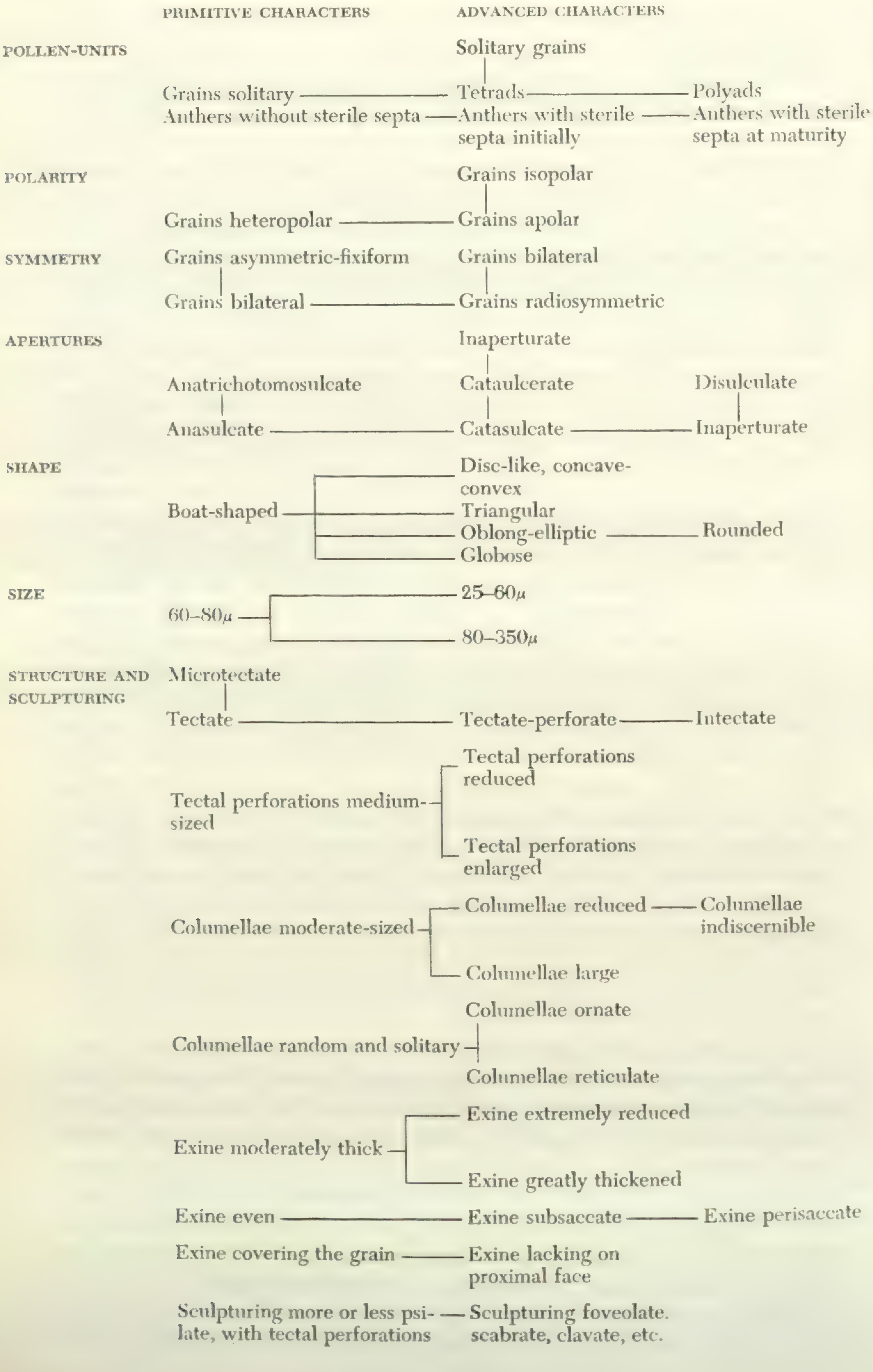
It is interesting to note that while the genus *Pseudoxandra* clearly has a most primitive aperture type within the family, it is already somewhat specialized with regard to exine sculpturing and structure and clearly shows a tendency toward the exine type found in the *Fusaea* group.

Table 7 summarizes the primitive and advanced pollen characters for the family.

Selective Value (Adaptive Significance) of Pollen Characters

Like most other features of the plant, the majority of pollen characters are probably the result of natural selection. In some instances, support may be found for a certain hypothesis concerning the selective value of a given pollen character by use of correlation studies, as was done by Grant (1950) with regard to the evolution of epigynous flowers. In other cases actual experiments may be conducted to determine the selective value of a pollen character (Whitehead, 1969). However, the determination of the selective value of some characters may not be open to experimentation, and their selective value may always be a matter of question and debate. The following discussion consists mainly of suggested selective values for certain pollen characters and is intended primarily to provoke further

TABLE 7. PRIMITIVE AND ADVANCED POLLEN CHARACTERS IN THE ANNONACEAE



discussion. It is hoped that it may lead to future experimentation which may give quantitative answers for some of the proposed hypotheses.

From a survey of the genera and families of angiosperms in which pollen tetrads and polyads occur (table 1), it appears that the evolution of these pollen-units correlates significantly with a high ovule number per ovary.[11] The only two angiosperm families which have pollinia (the *Orchidaceae* and *Asclepiadaceae*) are both characterized by having numerous seeds per ovary. In the *Orchidaceae* especially, the number of seeds per capsule reaches fantastic proportions. The *Ericaceae*, which is a family well-known for its pollen tetrads, is also well-known for its numerous, small seeds.

Within the *Annonaceae* this correlation is quite evident. For example, in the related genera *Anaxagorea* and *Xylopia*, the former has solitary pollen and two ovules per carpel, while the latter has pollen in tetrads or polyads and several to many ovules per carpel. Another example of the connection between ovule number and the occurrence of tetrads may be seen in the two closely related genera, *Hexalobus* and *Cleistochlamys*. *Hexalobus* has numerous ovules and cataulcerate tetrads, while in *Cleistochlamys* the ovule number has been reduced to one per carpel and the pollen grains have become solitary and inaperturate.

It is clear that the single, basal ovule in each carpel of the genus *Annona* represents an end line from ancestors that had numerous ovules in each ovary. It is interesting in this connection to note that there is a progressive trend within the genus toward the reduction of the tetrads and their final loss with the development of inaperturate, solitary grains in the advanced West Indian species of *Annona*. The two closely related, uniovulate genera, *Rollinia* and *Rolliniopsis*, produce only solitary grains.

The most dramatic correlation of high ovule number with large pollen-units is seen, however, in *Cymbopetalum* and its relatives. Here, fruits with numerous seeds reach some of the greatest dimensions in the family. In this group of genera the occurrence of polyads is a constant feature, with one genus having as many as 24 pollen grains in a single unit.

There is no apparent reason why septate stamens should be constantly correlated in the family with tetrads or polyads, but the fact that the stamens of the genera of *Mimosoideae* with polyads are also septate speaks for a common basis, if nothing more than developmental necessity.

The initial evolution of the pollen aperture itself was certainly in response to the need for a more efficient means of exit for the germinating pollen tube; but, as Wodehouse (1935) has pointed out, the aperture also serves a harmomegathic function in permitting changes in the volume of the grain with varying humidity.

The original monosulcate grains were rather limited in this latter respect according to Wodehouse, who saw the development of the basic tricolpate pollen of the angiosperms as . . .

[11]This idea was first suggested to the author by Dr. James A. Doyle.

> the great achievement of the dicotyledonous pollen grain. With it the grain was released from the limitations imposed upon it by the single long, deep furrow of the monocolpate form of grain which had been its heritage from the pteridosperms of the remotest antiquity. With this release came the most surprising diversity of form, through the relatively short succeeding span in the evolutionary scale, standing in remarkable contrast to the continuous monotony of the preceding development of the one-furrowed grain which we have traced step by step from the pteridosperms to the Magnoliaceae.
>
> (Wodehouse, *Pollen Grains*, pp. 330–331)

However, another equally important reason for the development of tricolpate and multi-furrowed, multi-pored grains may be given. In the gymnosperms with their unenclosed ovules and pollination droplet the direction of the germinating pollen tube was probably not very critical due to the moist environment of the pollination chamber. The orientation of the pollen grain on the stigma of an angiosperm, however, would seem to be of some concern. Even with stigmatic papillae, it would appear likely that those pollen grains with the pollen tube germinating in the direction of the stigmatic surface would be favored. A monosulcate, boat-shaped grain could easily germinate in the direction away from the stigmatic surface and perish from the lack of moisture, while a tricolpate, more or less globose grain would appear to have a better chance of germinating near the stigmatic surface and hence of avoiding desiccation.

The trend within the *Annonaceae* toward the loss of exine on the proximal face of the grains in the polyads of *Cymbopetalum* and its relatives would appear to lend support to this idea. With a polyad of over 400μ, as in some species of *Cymbopetalum*, one can readily see the disadvantage of pollen tubes germinating in all directions in the air and the advantage of the lack of exine on the inner faces of the grains, with the contiguous intine providing a moist, internal milieu for the downward germination of the mass of pollen tubes. This idea could easily be followed up and verified in the field.

Since grain polarity, symmetry, and shape are all more or less tied up with aperture type, they will not be discussed independently.

The size of pollen grains appears to be most closely related to the means of pollination—whether by insects (entomophily) or wind (anemophily). Whitehead (1969) says that the syndrome of an anemophilous plant includes the production of large numbers of pollen grains, pollen grains with thin exine and smooth sculpturing, and grains in the size range of 20–40μ. Grains larger than 40μ drop too soon in air currents, while grains less than 20μ are swept around the stigma and fail to be caught on the receptive stigmatic surfaces.

The large size of most annonaceous pollen with its sometimes enormously thick, highly sculptured exine suggests a high degree of insect pollination. Field studies on the pollination mechanisms in the family would be of high interest in light of the information now known concerning trends of specialization of its pollen. The means of pollination in the genus *Guatteria*, with its highly reduced exine and disulculate grains,

should be of particular concern to future field workers. The grains of this genus are remarkable for a non-aquatic, tropical tree because of the extremely reduced exine. Whatever the pollination method, it must be eminently successful since *Guatteria,* with its 250 species, is the largest genus in the family.

In general, wind pollinated species have smooth, dry pollen, while entomophilous plants have highly sculptured, oily pollen grains. It would appear that the most significant selective value of sculpturing is simply its presence and that the myriads of diverse sculpturing types (clavate, verrucate, echinate, etc.) all represent different ways of accomplishing the same goal, namely, the transfer (via insects) of a limited number of pollen grains from a stamen to a stigma with least loss and with the highest degree of efficiency. The fact that oily, highly sculptured pollen grains tend to stick together in masses would also be of selective value in such highly specific pollination methods as certain forms of entomophily.

The selective advantage of internal structural differences (columellae arrangements, etc.) is hard to visualize, but may be related to the development of more effective supporting devices for the tectum and its sculpturing elements.

PHYTOGEOGRAPHY

The family *Annonaceae* is a predominantly tropical group of some 130 genera and approximately 2,300 species. There are three centers of distribution among which the genera are more or less evenly divided—America, with some 36 endemic genera, Africa (including Madagascar) with some 40 endemic genera, and Asia with approximately 50 endemic genera (cf., table 8). One genus occurs in all three centers *(Xylopia),* three occur in both Asia and Africa *(Uvaria, Polyalthia, Artabotrys),* one is found in both Asia and America *(Anaxagorea),* and one in both Africa and America *(Annona).*

Both floral morphology and pollen morphology provide strong evidence for the origin of the family *Annonaceae* in the American tropics (or possibly Africa), with the major center in the Amazon Basin and a secondary center in Central America. Outlying areas of distribution include the islands of the West Indies, the drier regions of southern Brazil, Paraguay, and (rarely) Argentina, and the drier parts of Central America and Mexico. Eastern North America is another outlying area of distribution with two genera, *Asimina* and *Deeringothamnus.*

Of the 10 recognized palynological groups within the family (considering the *Fusaea* group as one), nine are found in the American center of distribution, while six are either endemic or have the majority of their members in the New World (cf., table 9). Africa has only one palynological group with most of its members found there (the *Hexalobus* group), while Asia has only two groups (the echinates and inaperturates) with the majority of their members endemic or highly restricted to the Asian region.

TABLE 8. GEOGRAPHICAL DISTRIBUTION OF THE GENERA OF THE ANNONACEAE

AMERICA (36–593)*

Cremastosperma 17†, Malmea 14, Ephedranthus 4, Pseudephedranthus 1, Pseudoxandra 6, Oxandra 25, Ruizodendron 1, Unonopsis 33, Bocageopsis 3, Onychopetalum 4, Desmopsis 16, Stenanona 2, Reedrollinsia 1, Sapranthus 12, Tridimeris 1, Tetrameranthus 2, Duguetia 74, Guatteria 250, Guatteriella 1, Guatteriopsis 4, Heteropetalum 2, Duckeanthus 1, Fusaea 3, Diclinanona 2, Asimina 8, Deeringothamnus 2, Raimondia 4, Rollinia 65, Rolliniopsis 4, Cymbopetalum 13, Cardiopetalum 1, Froesiodendron 2, Porcelia 5, Trigynaea 5, Bocagea 2, Hornschuchia 3.

AFRICA (40–255)

Enantia 10, Pachypodanthium 3, Polyceratocarpus 8, Cleistopholis 4, Friesodielsia** 15, Monanthotaxis 4, Enneastemon 10, Popowia** 65, Gilbertiella 1, Atopostema 2, Exellia 1, Xylopiastrum 1, Balonga 1, Letestudoxa 2, Afroguatteria 2, Toussaintia 3, Dielsiothamnus 1, Fenerivia 1, Pseudartabotrys 1, Greenwayodendron 2, Lettowianthus 1, Piptostigma 15, Neostenanthera 6, Boutiquea 1, Mkilua 1, Pseudannona 2, Meiocarpidium 1, Uvariastrum 7, Uvariopsis 13, Monocyclanthus 1, Dennettia 1, Cleistochlamys 1, Uvariodendron 14, Hexalobus 5, Asteranthe 2, Ophrypetalum 1, Monodora 20, Isolona 20, Mischogyne 2, Anonidium 4.

ASIA (50–662)

Desmos 25, Dasymaschalon 12, Friesodielsia** 40, Anomianthus 1, Tetrapetalum 2, Ellipeia 5, Ellipeiopsis 2, Cyathostemma 8, Rauwenhoffia 5, Dasoclema 1, Enicosanthum 16, Sageraea 9, Stelechocarpus 5, Kingstonia 1, Trivalvaria 6, Fitzalania 1, Mezzettia 7, Chieniodendron 1, Haplostichanthus 1, Monocarpia 1, Cyathocalyx 15, Drepananthus 10, Meiogyne 8, Oncodostigma 3, Guamia 1, Papualthia 20, Woodiella 1, Fissistigma 80, Mitrella 5, Melodorum 3, Pyramidanthe 1, Alphonsea 30, Miliusa and Saccopetalum 40, Phaeanthus 20, Marsypopetalum 1, Orophea 60, Platymitra 2, Mitrephora 40, Pseuduvaria 35, Petalolophus 1, Oreomitra 1, Schefferomitra 1, Polyaulax 1, Popowia** 40, Neouvaria 2, Cananga 2, Goniothalamus 80, Richella 2, Disepalum 8.

AMERICA, AFRICA, AND ASIA (1–170): Xylopia 170.
AFRICA AND ASIA (3–425): Uvaria 175; Polyalthia 150; Artabotrys 100.
AMERICA AND ASIA (1–29): Anaxagorea 29.
AMERICA AND AFRICA (1–125): Annona 125.

*Number of genera and approximate number of species.
†Approximate number of species.
***Popowia* and *Friesodielsia*, as presently constituted, have species in Africa and Asia. However, there is good evidence that four genera instead of two are involved and that none of them occur both in Africa and in Asia.

The rare and very primitive pollen type within the family that has retained the sulcus on the distal face (anasulcate) is entirely New World, while the great majority of the sulcate types of the primitive *Malmea* tribe (presumably catasulcate) are American (10 genera with some 100 species). There is only one African genus *(Enantia)* in this tribe.

By contrast the *Uvaria* tribe, with its advanced inaperturate and echinate pollen types, is heavily represented in Asia and to a lesser degree in Africa. Of 47 inaperturate and echinate genera in this tribe, only five are American.

The *Guatteria* tribe with its disulculate pollen is entirely American, while the whole *Annona* subfamily is decidedly American with the exception of the *Hexalobus* tribe.

The *Fusaea* subfamily is more or less evenly distributed among the three centers of distribution. However, within the bicentric genus

Pollen Type	New World	Asia	Africa
Anasulcates (1) *	■		
Catasulcates (12)	■	—	▬
Echinates (6)		■	▬
Inaperturates (41)	—	■	—
Disulculates (4)	■		
Cataulcerates			
Fusaea-type			
Anaxagorea & Piptostigma (2)	■	—	—
Xylopia (1)	▬	▬	▬
Fusaea-Goniothalamus Group (7)	—	■	▬
Annona-type			
Hexalobus Group (7)	—		■
Asimina Group (2)	■		
Annona Group (4)	■		—
Cymbopetalum Group (6)	■	—	

* number of genera

TABLE 9. GEOGRAPHICAL DISTRIBUTION OF ANNONACEOUS POLLEN TYPES

Anaxagorea, not only the bulk of the species are American rather than Asian (23 species versus 6 species), but the American species also have the most primitive stamens in the family (laminar and leaf-like).

Thus, the American center is characterized not only by having the overwhelming majority of primitive pollen types, but by having the greatest diversity of pollen types within the family as well.[12] By contrast the Asian genera are almost all highly specialized palynologically (and florally),[13] the great majority having inaperturate or echinate pollen. There is only one sulcate genus in Asia other than the fusaeoid genus *Anaxagorea,* and it is monotypic and advanced *(Monocarpia).* The entire *Annona* subfamily has only a single Asian genus *(Disepalum)* with some eight species, and this genus is highly advanced even within the *Annona* subfamily. It was a surprise to the author to come to the conclusion that the *Annonaceae* were of New World (and/or possibly African) origin in light of the fact that the great majority of primitive angiosperm families are clearly of an Asian or Australasian origin.[14]

Palynologically, the African genera are more diverse than those of Asia, which are for the most part rather monotonous with their predominantly inaperturate type of pollen. It appears as if a number of different groups reached Africa from the main center of evolution in South America, although they may possibly represent relic groups from the original center of origin. However, the bulk of Asian genera seems to represent an adaptive radiation from one or a few closely related types. Finally, mention should be made of the strong representation of the *Hexalobus* tribe of the *Annona* subfamily in Africa and Madagascar.

Thus, Africa has a high number of what may be relic genera, and since material of some 21 African genera was not available at the time of the present study, one cannot rule out the possibility of Africa or Africa–South America (with subsequent continental drift) as being the primary center of origin for the family, rather than South America alone. One can, however, state with some confidence that the data from both pollen and floral morphology preclude an Asian-Australasian origin for the family.

Finally, it is interesting to note that the three closely related families, *Annonaceae, Canellaceae,* and *Myristicaceae* (which I recognize as the order *Annonales*), all appear to have a neotropical and/or African origin, unlike most other "ranalean" families, such as the *Magnoliaceae, Winteraceae, Degeneriaceae,* etc. The *Canellaceae* is entirely American-African with no Asian representatives, while the *Myristicaceae* are more or less

[12]The author agrees with Smith (1967) that both the morphological diversity and comparative primitiveness within such families as the *Winteraceae, Magnoliaceae, Illiciaceae, Schisandraceae,* and *Monimiaceae* are greater among the Asian representatives than among those of America; however, strong exception must be taken to his inclusion of the *Annonaceae* in the above list of families.

[13]It is surely not an insignificant fact that a great number of Asian *Annonaceae* are climbers. **whereas a scandent habit is almost unknown in the American species.**

[14]In this connection it was of some interest to discover that Ehrendorfer *et al.* (1968), on the basis of chromosome numbers within the *Annonaceae,* suggest that the neotropic regions may be the **center for the family.**

evenly divided among the tropics of America, Africa, and Asia. *A priori*, one might assume (as the present author did before this investigation) that the Asian-Australasian genera of *Myristicaceae* are the most primitive in the family. However, it has been learned from Dr. T. K. Wilson, via personal communication, that his preliminary studies on the floral morphology of the family seem to indicate that the American genera are more primitive than those of Asia. Thus, it appears that the order *Annonales*, consisting of the families *Annonaceae*, *Canellaceae*, and *Myristicaceae*, has phytogeographical unity as well as similarities in the floral and pollen morphology.

PHYLOGENY

Informal Infrafamilial Classification

The following proposed informal classification of the *Annonaceae* is based primarily upon pollen morphology and to a lesser extent upon floral morphology and phytogeography. Three subfamilies and seven tribes are presently recognized. The hierarchical categories are only informally proposed at this time because it is desirable to defer erecting a formal nomenclature until further morphological studies of the *Annonaceae* now in progress are complete. The *Malmea* subfamily contains three tribes: the *Malmea*, *Uvaria*, and *Guatteria* tribes. No tribes are currently recognized within the *Fusaea* subfamily. The *Annona* subfamily has four tribes: the *Hexalobus*, *Asimina*, *Annona*, and *Cymbopetalum* tribes (cf., table 10).

Table 10. proposed informal classification of the annonaceae

I. Malmea Subfamily
   1. malmea tribe: Cremastosperma, Malmea, Ephedranthus, Pseudephedranthus, Pseudoxandra, Oxandra, Ruizodendron, Unonopsis, Bocageopsis, Onychopetalum, Enantia.
   2. uvaria tribe: Desmopsis, Stenanona, Reedrollinsia, Sapranthus, Tetrameranthus, Duguetia, Polyceratocarpus, Cleistopholis, Friesodielsia (African), Monanthotaxis, Enneastemon, Popowia (African), Desmos, Dasymaschalon, Friesodielsia, Uvaria, Anomianthus, Tetrapetalum, Ellipeia, Cyathostemma, Rauwenhoffia, Enicosanthum, Sageraea, Stelechocarpus, Trivalvaria, Polyalthia, Mezzettia, Chieniodendron, Artabotrys, Monocarpia, Cyathocalyx, Drepananthus, Meiogyne, Oncodostigma, Guamia, Papualthia, Woodiella, Fissistigma, Mitrella, Melodorum, Alphonsea, Miliusa, Saccopetalum, Phaeanthus, Orophea, Platymitra, Mitrephora, Pseuduvaria, Popowia, Neouvaria.
   3. guatteria tribe: Guatteria, Guatteriopsis, Heteropetalum.

II. Fusaea Subfamily
   Anaxagorea, Piptostigma, Neostenanthera, Xylopia, Duckeanthus, Fusaea, Meiocarpidium, Cananga, Goniothalamus, Richella.

III. Annona Subfamily
   1. hexalobus tribe: Uvariastrum, Uvariopsis, Cleistochlamys, Hexalobus, Monodora, Isolona, Diclinanona.
   2. asimina tribe: Asimina, Deeringothamnus.
   3. annona tribe: Annona, Raimondia, Rollinia, Rolliniopsis.
   4. cymbopetalum tribe: Cymbopetalum, Cardiopetalum, Porcelia, Trigynaea, Hornschuchia, Disepalum.

TABLE 11. NUMBER OF GENERA AND SPECIES IN THE PROPOSED SUBFAMILIES AND TRIBES OF THE ANNONACEAE

	Genera	Species
I. MALMEA SUBFAMILY	64	1570
1. Malmea Tribe	11	118
2. Uvaria Tribe	50	1196
3. Guatteria Tribe	3	256
II. FUSAEA SUBFAMILY	10	310
III. ANNONA SUBFAMILY	19	311
1. Hexalobus Tribe	7	68
2. Asimina Tribe	2	10
3. Annona Tribe	4	198
4. Cymbopetalum Tribe	6	35

Table 11 gives the approximate number of genera and species in each subfamily and tribe, while table 12 is a synoptical, palynological key to the subfamilies and tribes proposed.

The *Malmea* subfamily is characterized by sulcate, inaperturate, or disulculate pollen which is only very rarely in tetrads *(Pseudoxandra, Mitrephora,* and *Pseuduvaria).* The columellae are usually medium-sized, although they are so highly reduced as to be indiscernible in the *Guatteria* tribe. The tectal perforations, when present, also tend to be moderate in size. Florally this subfamily is very diverse, but no septate stamens or syncarps occur in it.

The *Malmea* tribe is composed entirely of genera with sulcate pollen and is without doubt the most primitive tribe palynologically (and also in many aspects of its floral morphology) within the family.

One genus of the *Malmea* tribe, *Pseudoxandra,* is the only one in the family to have retained the primitive anasulcate condition. The other genera are presumed to be catasulcate, but this has only been shown for one species, *Cremastosperma cauliflorum* (Canright, 1963). While *Pseudoxandra* is very primitive with regard to its aperture type, its columellae and tectal perforations appear to be somewhat advanced in the direction of the *Fusaea* subfamily. The basic sculpturing pattern for the tribe (and the family) is considered to be that shown by such genera as *Malmea, Cremastosperma,* and *Unonopsis,* with both moderate-sized columellae and tectal perforations.

Palynologically, the genera *Cremastosperma, Malmea, Ephedranthus, Pseudephedranthus, Unonopsis, Bocageopsis, Monocarpia,* and *Enantia* form a close-knit group with their usually highly reticulate columellae and well-developed tectate-perforate grains. The genera *Oxandra, Ruizodendron,* and *Onychopetalum* depart from this basic pattern with their tendency toward becoming subsaccate or even strongly perisaccate *(Onychopetalum)* and their reduced columellae. The latter three genera are also characterized by smaller grain size. The moderately specialized structure and sculpturing of *Pseudoxandra,* which is combined with a very primitive aperture type, has already been mentioned. Finally, the mono-

TABLE 12. SYNOPTICAL PALYNOLOGICAL KEY TO THE SUGGESTED SUBFAMILIES AND TRIBES OF THE ANNONACEAE

I. Pollen grains sulcate, inaperturate, or disulculate; mostly solitary, rarely in tetrads; columellae usually medium-sized; tectal perforations, if present, moderate-sized . . . . . *Malmea* Subfamily.
   A. Pollen grains sulcate and not echinate . . . . . *Malmea* Tribe.
   B. Pollen grains inaperturate, sulcate and echinate, or disulculate, rarely sulcate.
      1. Pollen grains inaperturate, sulcate or inaperturate and echinate, or rarely disulculate with reduced but distinct columellae, rarely sulcate. . . . *Uvaria* Tribe.
      2. Pollen grains disulculate with highly reduced exine and no columellae discernible . . . . . *Guatteria* Tribe.

II. Pollen grains cataulcerate (sometimes sulcate or catasulcate), occasionally inaperturate; mostly in tetrads (or polyads), rarely solitary; columellae indiscernible or very large; tectal perforations either very pronounced or highly reduced to pits.
   A. Columellae very indistinct or indiscernible . . . . . *Fusaea* Subfamily.
   B. Columellae distinct, usually very large . . . . . *Annona* Subfamily.
      1. Pollen grains in tetrads (rarely solitary).
         a. Longest axis of pollen grains rarely more than 70μ; mainly African . . . . . *Hexalobus* Tribe.
         b. Longest axis of pollen grains usually more than 80μ.
            (1) Tectal perforations usually pronounced, from 4–12μ; grains never inaperturate; United States and Canada . . . . . *Asimina* Tribe.
            (2) Tectal perforations usually not as pronounced; grains sometimes inaperturate; tropical America, rarely Africa . . . . . *Annona* Tribe.
      2. Pollen grains in polyads . . . . . *Cymbopetalum* Tribe.

sulcate grains of *Polyceratocarpus* with their fragile aperture and small columellae are distinctive.

The *Malmea* tribe is mostly American, with 10 of its 11 genera endemic to the New World. One genus *(Enantia)* is African. Only three genera in this tribe have more than one ovule per carpel, and they are *all* among the valvate, not the imbricate-petaled, genera. This would seem to imply that a low ovule number may be primitive for the family and that genera with numerous ovules may have acquired them secondarily. *Unonopsis* is the only genus in the tribe to have either several ovules or one ovule per carpel, and may show the transition from low to high ovule number. A floral character which is quite prevalent in this tribe is the occurrence of bracts both below and above the articulation in the peduncle. The rounded petals of *Cremastosperma* and *Malmea* appear to be primitive for the family and are reminiscent in size, shape, and texture of the petals of *Degeneria.*

The *Uvaria* tribe is composed mainly of genera with inaperturate pollen but includes a few genera with sulcate and one with disulculate pollen. Palynologically, this tribe is very monotonous with its predominantly inaperturate type of pollen. Two genera have inaperturate grains in tetrads *(Mitrephora* and *Pseuduvaria).* Three *(Desmos, Dasymaschalon,* and *Friesodielsia)* are quite distinctive with their strongly echinate pollen which may be sulcate or inaperturate. Three genera with predominantly inaperturate pollen *(Uvaria, Artabotrys,* and *Polyalthia)* have retained sulcate pollen in a few species, although the sulcus may be reduced and

vestigial. Finally, one genus *(Sapranthus)* has disulculate pollen along with a rather reduced exine.

Uvaria, Anomianthus, Tetrapetalum, and *Cyathostemma* form a group within the tribe on the basis of their somewhat reduced exine, which often has a wavy appearance. Some of the genera are quite verrucate. A further study of sculpturing types might lead to a better understanding of the interrelationships within this tribe. *Duguetia* is notable for its highly reduced exine which must be prepared for study by KOH-treatment rather than by the standard acetolysis method. The pollen of *Tetramerianthus* is remarkable for its high degree of psilateness. The pollen of *Monanthotaxis, Enneastemon,* and the African species of *Popowia* is distinctive with its microbaculate sculpturing.

Phytogeographically, the *Uvaria* tribe is predominantly Asian, with only six American genera out of a total of 50. The tribe is florally diverse, although no syncarps occur among its genera. Mention should be made of the occurrence of clawed, mitriform petals in one group of evidently closely related genera (*Orophea, Mitrephora, Pseuduvaria,* etc.). The author intends to divide this large tribe into subtribes in a subsequent paper. However, to do so now, with further studies on the *Annonaceae* in progress, would be premature.

The third tribe of the *Malmea* subfamily is the *Guatteria* tribe with only three genera, but some 250 species. Its pollen is highly distinctive, being disulculate and with a strongly reduced exine. All members of this tribe have bracts below the articulation in the peduncle and none above, and all have a solitary, basal ovule. They are entirely New World.

The *Fusaea* subfamily, which is characterized by cataulcerate pollen usually in tetrads (or polyads), has the columellae reduced so as to be indiscernible. The trend toward pollen gigantism is evident. The anthers are septate in a number of genera and the pollen is solitary in only two *(Anaxagorea* and *Piptostigma).*

The fruit type of *Anaxagorea* is unique in the family in being a dehiscent follicle with two seeds. Again, this low seed number is taken as a primitive character and the dry, dehiscent fruit is considered to represent a primitive type within the family, reminiscent of the *Magnoliaceae.* The genus *Anaxagorea* is also remarkable for its primitive, laminar, non-peltate stamens, which are without doubt the most primitive stamens extant within the family. The pollen of *Xylopia* (as well as its fruit type—a dehiscent berry) is somewhat intermediate between that of *Anaxagorea* and the rest of the subfamily. Phytogeographically, this subfamily is represented in all three world centers of distribution. Its antiquity may be seen in the unique, bicentric distribution of *Anaxagorea* (America and Asia) and in the unique, tricentric distribution of *Xylopia* (America, Africa, and Asia).

The *Annona* subfamily has four tribes. The pollen is predominantly cataulcerate or rarely secondarily inaperturate. It is remarkable for its large to gigantic columellae as well as for very prominent tectal perfora-

tions. The grains are mostly in tetrads or polyads. There is a very strong trend toward pollen gigantism, as well as toward septate stamens. The subfamily is almost entirely American with the notable exception of the first and presumably most primitive tribe (the *Hexalobus* tribe), which is centered in Africa.

The *Hexalobus* tribe exhibits all the initial trends so common in this subfamily as a whole. It, along with the majority of the genera of two of the other tribes (the *Asimina* and *Cymbopetalum* tribes), has numerous ovules in most of its species. Only the *Annona* tribe itself is characterized by a single ovule in each carpel. Thus, numerous ovules appear to be basic in this subfamily, in contrast to the other two.

Monodora and *Isolona* are the only genera in the family with a unilocular, compound pistil with parietal-laminar placentation. This may represent (along with the *Canellaceae*) one of the few instances in the angiosperms of primary parietal placentation as opposed to parietal placentation secondarily derived from axile placentation.

The *Asimina* tribe is composed of two small genera, *Asimina* and *Deeringothamnus*, both entirely North American. Their pollen grains are somewhat larger than those in the preceding tribe. They have much larger columellae and are much more evidently tectate-perforate. The membranous petals that are often wrinkled are reminiscent of those of *Hexalobus* and its allies.

The *Annona* tribe retains pollen in its more primitive members (*Annona* sect. *Annona*) which is quite similar to that of *Asimina*. However, this tribe is characterized by syncarpous fruits and large, thick, fleshy petals, which are highly reminiscent of *Porcelia* and *Cymbopetalum* in the next tribe. Solitary, inaperturate pollen characterizes the more advanced sections of *Annona*, as well as the closely related genera *Rollinia* and *Rolliniopsis*. The tribe is entirely American except for a few African species of *Annona*.

The last tribe, the *Cymbopetalum* tribe, is characterized by polyads and septate stamens (except in *Disepalum*). The fruits of the more primitive members are highly reminiscent of those of *Asimina*, while the petals show similarity, as mentioned before, with *Annona*. The fruit of *Cymbopetalum* is distinctive in that it opens laterally. An almost constant feature in this tribe is the totally ebracteate peduncle of the flowers. Arillate seeds are also of frequent occurrence. In connection with the septate stamens found in *Cymbopetalum* and its allies, it is interesting to note that Herms (1907), Samuelsson (1914), and Lecomte (1896) found what may be interpreted as rudimentary septa, which break down by the time the pollen tetrads are mature, in the developing stamens of *Asimina*, *Annona*, and *Monodora* respectively. *Disepalum* is somewhat separated from the other members of this tribe with its non-septate anthers (at least at maturity) and solitary ovule. The tribe is entirely American with the exception of *Disepalum*, which is Asian.

Previous Infrafamilial Classification

There are two modern, world-wide treatments of the *Annonaceae:* Fries, 1959; and Hutchinson, 1964. Sinclair's revision of 1955 covers only the Malayan members of the family. Other papers important for the classification of the family include Diels (1932) and Fries (1942). Table 13 gives a summary of the subfamilial and tribal treatments of the family by Fries, Hutchinson, and Sinclair. They all agree in recognizing two subfamilies, the *Annonoideae* and the *Monodoroideae,* which has only two genera, *Monodora* and *Isolona*. They also recognize two major tribes, the *Uvarieae* and the *Unoneae,* which are distinguished solely on the character of imbricate versus valvate aestivation of the petals. The only major difference among the three systems is the recognition by Hutchinson and Sinclair of a tribe *Miliuseae* and its rejection by Fries, with the statement that it is a very unnatural tribe, being based upon the single character of reduced, sepaloid, outer petals.

The systems of Sinclair and Hutchinson are very artificial, as Hutchinson himself admits, and are largely patterned after the classification of Bentham and Hooker. Hutchinson's *Miliuseae* is an extremely unnatural taxon, basically containing not only a number of genera with inaperturate pollen of the *Uvaria* tribe, but also *Heteropetalum* of the *Guatteria* tribe, *Piptostigma* of the *Fusaea* subfamily, and *Cymbopetalum* of the *Annona* subfamily. Thus Hutchinson, by using a single floral character, has combined genera with inaperturate, disulculate, sulcate, and cataulcerate-

TABLE 13. SUMMARY OF SOME FORMER INFRAFAMILIAL CLASSIFICATIONS OF THE ANNONACEAE

Fries (1959)	Hutchinson (1964)	Sinclair (1955)
Annonoideae	Annonoideae	Annonoideae
Uvarieae	Uvarieae	Uvarieae
Uvaria Group	Miliuseae	Miliuseae
Duguetia Group	Unoneae	Unoneae
Asimina Group	Xylopiinae	Xylopieae
Hexalobus Group	Group A	Mitrephoreae
Guatteria Group	Group B	Annoneae
Unoneae	Group C	Monodoroideae
Desmos Group	Annoninae	
Polyalthia Group	Monodoroideae	
Unonopsis Group		
Xylopia Group		
Artabotrys Group		
Orophea Group		
Annona Group		
Trigynaea Group		
Monanthotaxis Group		
Tetramerantheae		
Monodoroideae		

polyad pollen all in the same tribe. By contrast Fries, in his system, correctly placed *Piptostigma* next to *Anaxagorea, Heteropetalum* next to *Guatteria,* and *Cymbopetalum* in the same group with the other polyad

genera with septate stamens. We may dispense with further consideration of Hutchinson's system and turn to the only modern, world-wide classification of the *Annonaceae* which is partially natural, that of Fries.

Although Fries relied predominantly upon floral morphology, it is evident that his life-long experience with the family led him to select characters which, on the whole, are more useful in erecting a natural classification of the family than those used by Hutchinson. Fries proposes 14 "groups" which are comparable to tribes. The greatest weakness of his system is that he still recognizes a primary division based on petal aestivation. Characters that he uses which often lead to the recognition of natural groups include: the location of bracts on the peduncle, the type and position of the inflorescence, the number of ovules per carpel, and the occurrence of septate stamens. The naturalness of a number of Fries' "groups" has been confirmed by their pollen morphology. This is especially true of his *Uvaria, Guatteria, Annona,* and *Trigynaea* groups. However, his use of a single floral character often led to the separation of closely related genera, e.g., *Malmea* and *Cremastosperma; Desmos, Dasymaschalon.* and *Friesodielsia.*

Many of the tribes proposed in this study have their nucleus in one or more of Fries' "groups." The only infrafamilial taxon which is here proposed that has been totally unrecognized by all previous workers is the *Fusaea* subfamily. Its members, however, appear to have such distinctive and similar pollen in almost all characters as to strongly support the naturalness of the group. *Monodora* and *Isolona,* although isolated with reference to their unilocular, compound pistil, seem better placed. on the totality of their floral and palynological characters, as members of the *Hexalobus* tribe rather than in a separate subfamily of their own.

Table 14 lists the segregate genera of the *Annonaceae* and indicates their placement in the systems of Fries, Hutchinson, and Sinclair. Airy-Shaw's treatment in the newest edition of Willis' *Dictionary* (1966) is also recorded.

Among the New World genera, there is only one *(Geanthemum)* which is in dispute. Both Fries and Airy-Shaw submerge it into *Duguetia,* while Hutchinson recognizes it as a separate genus. The pollen is that of a typical member of the genus *Duguetia* and does not support the maintenance of *Geanthemum* as a separate genus. Mention should also be made that pollen morphology supports the separation of the genus *Deeringothamnus* from *Asimina.*

Palynological data which are relevant to other generic problems include the following:

1) Support the inclusion of *Brieya* in *Piptostigma.*
2) Do not support the inclusion of *Monocarpia* in *Cyathocalyx.*
3) Support the inclusion of *Saccopetalum* in *Miliusa.*
4) Support the close proximity of *Mitrella* to *Fissistigma.*
5) Support the inclusion of *Dasymaschalon* in *Desmos.*
6) Support the inclusion of *Drepananthus* in *Cyathocalyx.*

7) Definitely do not support the inclusion by both Fries and Hutchinson of *Friesodielsia* (as *Oxymitra*) in *Richella*.[15]

Comments on the Classification of Certain Genera Not Included in This Study

Some 39 genera of *Annonaceae* were not included in the present study because of a lack of palynological material. Together they contain only about 70 species, but the African ones especially may be very important in adding to our knowledge of the family. On the basis of floral descriptions and some palynological data in the literature, I would like to comment on or predict the following concerning the classification of certain of these genera:

1) that *Guatteriella* should have disulculate pollen with an extremely reduced exine if it is correctly placed by Fries next to *Guatteria*.

2) that *Bocagea* should have polyads and cataulcerate pollen with large columellae and large, tectal perforations if it is correctly placed by Fries near *Cymbopetalum*.

3) that *Froesiodendron* will have polyads and cataulcerate pollen with large columellae and large, tectal perforations since its septate stamens and other characters appear to indicate its proper assignment to the *Cymbopetalum* tribe.

4) that *Afroguatteria* should have inaperturate pollen with distinct columellae if Fries' placement of it in his "*Uvaria* group" is correct, or disulculate pollen with a highly reduced exine if Hutchinson is correct in submerging the genus into *Guatteria*.

5) that *Uvariodendron* will have cataulcerate pollen with large columellae and a tectate-perforate exine based on Fries' statement that the grains are in tetrads and based on its floral morphology and distribution, which all indicate its placement in the *Hexalobus* tribe.

6) that *Xylopiastrum* should have cataulcerate grains in tetrads or polyads with indiscernible columellae if it is closely related to *Xylopia*, or solitary, inaperturate grains if related to *Uvaria*.

7) that *Anonidium* will have cataulcerate tetrads with large columellae since it appears to be closely related to *Annona*.

Pollen Morphology and Interfamilial Relationships

A number of pollen characters found within the *Annonaceae* appear to indicate relationships with the pollen types of certain other "ranalean"

[15]This poses a nomenclatural problem in that *Oxymitra* is a later homonym of a hepatic genus. There was no problem if one considered the genus congeneric with *Richella*. This cannot be done, however, since the pollen clearly indicates that there is not even a close relationship between the two genera. Another name, *Friesodielsia*, was proposed for *Oxymitra* by van Steenis (1948), and the necessary new combinations were made by him in 1964. It was unfortunate that Fries (1959) made a number of new combinations with *Richella*, which must now be abandoned in light of the palynological evidence.

TABLE 14. DIFFERING TREATMENTS OF CERTAIN GENERA OF THE ANNONACEAE*

Genus	Fries (1959)	Hutchinson (1964)	Sinclair (1955)	Airy-Shaw (1966)
American				
Geanthemum	Duguetia	+	–	Duguetia
African†				
Afroguatteria	+	Guatteria	–	+
Cleistochlamys	+	Popowia	–	+
Xylopiastrum	+	Xylopia	–	Uvaria
Brieya	Piptostigma	+	–	+
Tetrastemma	Uvariopsis	+	–	Uvariopsis
Thonnera	Uvariopsis	+	–	Uvariopsis
Asian				
Fitzalania	+	Uvaria	–	+
Monocarpia	+	Cyathocalyx	+	+
Sphaerocoryne	+	Polyalthia	Melodorum Lour.	Melodorum Lour.
Marcuccia	Enicosanthum	+	Enicosanthum	Enicosanthum
Sphaerothalamus	Polyalthia	+	–	Polyalthia
Griffithianthus	Enicosanthum	+	Enicosanthum	Enicosanthum
Saccopetalum	Miliusa	+	Miliusa	Miliusa
Pyramidanthe	Fissistigma	Fissistigma	+	+
Mitrella	Fissistigma	Fissistigma	+	+
Ararocarpus	+	+	Meiogyne virgata	Meiogyne
Dasymaschalon	+	+	Desmos	+(–Desmos)
Drepananthus	+	+	Cyathocalyx	Cyathocalyx
Melodorum Lour.	Doubtful genus	–	+	=Polyalthia sp. +Mitrephora sp.
Friesodielsia	Richella	Richella	+ (as Oxymitra)	+

+ Accepted as a genus.
— Not treated.
* The listing of the generic names indicates those in which the various segregate genera are submerged by different authors. For example, the genus *Geanthemum* is accepted as a genus by Hutchinson, it is submerged into *Duguetia* by both Fries and Airy-Shaw, and is not treated by Sinclair.
† The genus *Atopostema* is included in *Popowia* by Le Thomas in the *Flore du Gabon*, No. 16 (1969).
Doubtful genera listed by Fries (1959): *Nephrostigma* Griff., *Pelticalyx* Griff., *Soala* Blanco, and *Tabraca* Norunha.

families. Within what may be called the Magnoliad line of primitive, "ranalean" families, four separate orders may be erected containing the following families:

MAGNOLIALES: Magnoliaceae, Degeneriaceae, Himantandraceae, Eupomatiaceae. ANNONALES: Annonaceae, Canellaceae, Myristicaceae. ARISTOLOCHIALES: Aristolochiaceae. LAURALES: Austrobaileyaceae, Trimeniaceae, Calycanthaceae, Amborellaceae, Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae.

The pollen of *Pseudoxandra,* especially of *P. coriacea* with its anasulcate and anatrichotomosulcate grains and somewhat reduced columellae, resembles the pollen found in the *Canellaceae* (and to some degree that of the *Magnoliaceae*). This type of pollen in the two families *(Canellaceae* and *Annonaceae)* may represent directly homologous pollen grains. The resemblance of other pollen types in the *Annonaceae* to the pollen of related "ranalean" families may be indicative of a phylogenetic relationship, but probably only through parallel evolution.

The pollen of certain genera of *Myristicaceae* shows some similarity with the pollen of the *Annona* subfamily with respect to the presence of large, prominent columellae. In this connection it would be of some interest to determine the exact position of the aperture in myristicaceous grains of this type. Other myristicaceous grains and some in the *Aristolochiaceae* resemble *Desmos* and its allies in their echinate sculpturing.

The somewhat reduced monosulcate grains of *Anaxagorea,* with no discernible columellae, resemble in many respects the pollen of the *Himantandraceae* and to a lesser extent that of the *Degeneriaceae,* and may be the result of parallel evolution. The development of numerous inaperturate pollen types within the *Annonaceae* probably reflects a common potential with the lauralean families, and is a trait that became fixed in the majority of the members of the latter group.

Finally, the discovery of disulculate grains within the family has an important bearing upon the relationship of the *Annonaceae* with the *Eupomatiaceae.* The disulculate pollen found in the *Eupomatiaceae,* with its reduced exine, more closely resembles that of *Guatteria* and its allied genera in the *Annonaceae* than it resembles *Calycanthus* in the *Laurales.* The occurrence of this pollen type in both families would appear to be another character that supports the relationship of *Eupomatia* with the *Annonaceae* rather than with the *Calycanthaceae,* especially since both families possess ruminate endosperm. The discovery of a number of disulculate genera within the *Annonaceae* negates the position taken by Canright (1963) relative to the relationships of the *Eupomatiaceae.*

SUMMARY

A detailed description of the range of pollen morphology within the family *Annonaceae* has been presented, in addition to a proposed classification of the family, which hopefully represents the most natural system to date. The main results of this study may be summed up as follows:

1) Morphological. For the first time a comprehensive study, with detailed, generic descriptions, has been undertaken on the pollen of the *Annonaceae.*

2) Taxonomic. A number of obviously misplaced species were discovered in the course of this study, e.g., two species of *Polyalthia* which belong in the genus *Disepalum,* species of *Orophea* which are probably species of *Pseuduvaria,* etc.

3) Phylogenetic. The family *Annonaceae* is eurypalynous enough to allow a complete reclassification at the subfamilial and tribal levels, based primarily on pollen morphology.

4) Evolutionary. The present study revealed a number of interesting evolutionary trends within the pollen of the family, and suggestions have been made concerning the selective value of many of these trends.

5) Phytogeographical. The study has revealed the rather surprising fact that there is very strong evidence, from both floral and pollen morphology, for the New World and/or possibly African origin of the *Annonaceae.*

In the course of the pollen survey a number of interesting discoveries were made. The most important of these include the following:

1) Disulculate apertures were found in a number of genera for the first time in the family. This has significance for the relationship between the *Annonaceae* and the *Eupomatiaceae.*

2) A number of genera were found to have an extremely reduced exine, quite remarkable for large, non-aquatic, tropical trees.

3) A natural group of genera was discovered which is characterized without exception by the pollen grains being in polyads.

4) Probably the largest known fixiform pollen grain in the angiosperms was discovered in *Cymbopetalum odoratissimum,* some grains of which reach 350μ.

5) Primitive, laminar, leaf-like, stomate-possessing stamens were found in the genus *Anaxagorea.* These are the only stamens in the family to show remains of the lateral vascular traces.

6) The *Fusaea* subfamily was first recognized because of a remarkably distinct pollen type common to a number of genera previously widely separated in classification systems.

7) An extremely interesting and probably unique trend was discovered in the tetrad and polyad genera, in which the entire proximal face of the pollen grain is ultimately lacking in exine, with the intine from different grains centrally contiguous (e.g., *Cymbopetalum*).

8) The primitive pollen type for the family (anasulcate) was discovered in the genus *Pseudoxandra* and the complete transition from anasulcate to catasulcate was observed among the species of this genus. The sulcus in other genera of *Annonaceae* was shown to be located on the proximal face in contrast to all other known "ranalean" monosulcates, in which the furrow is on the distal face of the grain.

9) The reversal of the normal trend from solitary grains to tetrads was discovered in the definitely secondary development of solitary grains from forms with tetrads among the advanced, West Indian species of the genus *Annona* and in the closely related, derived genera *Rollinia* and *Rolliniopsis.*

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LITERATURE CITED

Agababyan, V. Sh. 1967. O prorastanii mikrospor u roda *Annona*. Akad. Nauk Armyanskoy S.S.R. Biol. Zhurnal Armenii 20(12):77–80. (In Russian, with an Armenian summary.)

Airy-Shaw, H. K. (revisor). 1966. J. C. Willis' A Dictionary of the Flowering Plants and Ferns, ed. 7. Cambridge University Press, Cambridge, England.

Bailey, I. W. & C. G. Nast. 1943. The comparative morphology of the Winteraceae. I. Pollen and stamens. Jour. Arn. Arb. 24:340–346.

Bartlett, A. S. 1967. Palynological studies of Gatun Basin, Panama. (Unpublished doctoral thesis, Harvard University, Cambridge, Mass.)

Canright, J. E. 1953. The comparative morphology and relationships of the Magnoliaceae. II. Significance of the pollen. Phytomorphology 3:355–365.

———————. 1963. Contributions of pollen morphology to the phylogeny of some ranalean families. Grana Palynologica 4:64–72.

Cronquist, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin Company, Boston.

Davis, G. L. 1966. Systematic Embryology of the Angiosperms. John Wiley & Sons, Inc., New York.

Diels, L. 1932. Die Gliederung der Anonaceen und ihre Phylogenie. Akad. der wissenschaften, Berlin. (Sitzungsber. K. Preuss. Akad. d. Wiss., Berlin) Physik-math. Klasse pp. 77–85.

Ehrendorfer, F. et al. 1968. Chromosome numbers and evolution in primitive angiosperms. Taxon 17:337–353.

Erdtman, G. 1945a. Pollen morphology and plant taxonomy. III. *Morina* L. with an addition on pollen morphological terminology. Svensk. Bot. Tidskr. 39:187–191.

———————. 1945b. Pollen morphology and plant taxonomy. V. On the occurrence of tetrads and dyads. Svensk. Bot. Tidskr. 39:286–297.

———————. 1960. The acetolysis method—a revised description. Svensk. Bot. Tidskr. 54:561–564.

———————. 1966. Pollen Morphology and Plant Taxonomy. Angiosperms (An Introduction to Palynology. I.), corrected reprint of the edition of 1952 with a new addendum. Hafner Publishing Co., New York.

Faegri, K. & J. Iversen. 1964. Textbook of Pollen Analysis, 2nd revised edition. Hafner Publishing Co., New York.

Fries, R. E. 1930. (Actual date of publication, 1931.) Revision der Arten einiger Anonaceen-Gattungen. I. Acta Hort. Berg. 10:1–128.

———————. 1931. Revision der Arten einiger Anonaceen-Gattungen. II. Acta Hort. Berg. 10:129–341.

———————. 1934. Revision der Arten einiger Anonaceen-Gattungen. III. Acta Hort. Berg. **12**:1–220.
———————. 1937. Revision der Arten einiger Annonaceen-Gattungen. IV. Acta Hort. Berg. **12**:221–288.
———————. 1939. Revision der Arten einiger Annonaceen-Gattungen. V. Acta Hort. Berg. **12**:289–577.
———————. 1942. (Actual date of publication, 1943.) Einige Gesichtspunkte zur systematischen Gruppierung der amerikanischen Annonaceen-Gattungen. Arkiv Bot. 30A(8):1–31.
———————. 1959. Annonaceae *in* Die natürlichen Pflanzenfamilien, ed. 2, 17aII. Duncker & Humblot, Berlin.

Grant, V. 1950. The protection of ovules in flowering plants. Evol. **4**:179–201.

Herms, W. B. 1907. Contributions to the life history of *Asimina triloba*. Ohio Nat. **8**:211–217.

Hutchinson, J. 1964. The Genera of Flowering Plants. Vol. 1. Oxford University Press, London.

Kuprianova, L. A. 1967. Apertures of pollen grains and their evolution in angiosperms. Rev. Palaeobotan. Palynol. **3**:73–80.

Lecomte, H. 1896. Sur la formation du pollen chez les Anonacées. Bull. Mus. Hist. Nat. Année 1896:152–153.

Le Maout, E. & J. Decaisne. 1876. A General System of Botany (trans. by Mrs. Hooker). Longmans, Green & Co., London (original French edition, 1868).

Le Thomas, A. 1969. Annonaceae *in* Flore du Gabon, No. 16. Muséum National d'Histoire Naturelle, Paris.

Locke, J. F. 1936. Microsporogenesis and cytokinesis in *Asimina triloba*. Bot. Gaz. **98**:159–168.

Maheshwari, P. 1950. An Introduction to the Embryology of Angiosperms. McGraw-Hill Book Co., Inc., New York.

Miquel, F. A. G. 1856. Ebenaceae *in* Martius' Flora Brasiliensis, vol. 7. (For description of *Hornschuchia* see pp. 18–19, plate 7, fig. 12.)

Mohl, H. von. 1834. Beiträge zur Anatomie und Physiologie der Gewächse I. Uber den Bau und die Formen der Pollenkörner. Chr. Fischer und Comp. Bern.

Mueller, F. 1865–66. Fragmenta Phytographiae Australiae. Vol. 5. Melbourne.

Periasamy, K. & B. G. L. Swamy. 1959. Studies in the Annonaceae I. Microsporogenesis in *Cananga odorata* and *Miliusa wightiana*. Phytomorphology **9**:251–263.

Samuelsson, G. 1914. Über die Pollenentwicklung von *Anona* und *Aristolochia* und ihre systematische Bedeutung. Svensk. Bot. Tidskr. **8**:181–189.

Sinclair, J. 1955. A revision of the Malayan Annonaceae. Gard. Bull. Singapore **14**:149–516.

Smith, A. C. 1967. The presence of primitive angiosperms in the Amazon Basin and its significance in indicating migrational routes. Atas do Simpósio sôbre a Biota Amazônica, vol. 4 (Botânica):37–59.

Sorsa, P. 1969. Pollen morphological studies on the Mimosaceae. Ann. Bot. Fenn. **6**:1–34.

Steenis, C. G. G. J. van. 1948. (Actual date of publication, 1949.) Remarks on some generic names used for Malaysian phanerogams. I. Bull. Bot. Gard. Buitenz. series 3. **17**:457–464.
———————. 1964. An account of the genera *Richella* A. Gray and *Oxymitra* (Bl.) Hook.f. & Th. (Annonaceae). Blumea **12**:353–361.

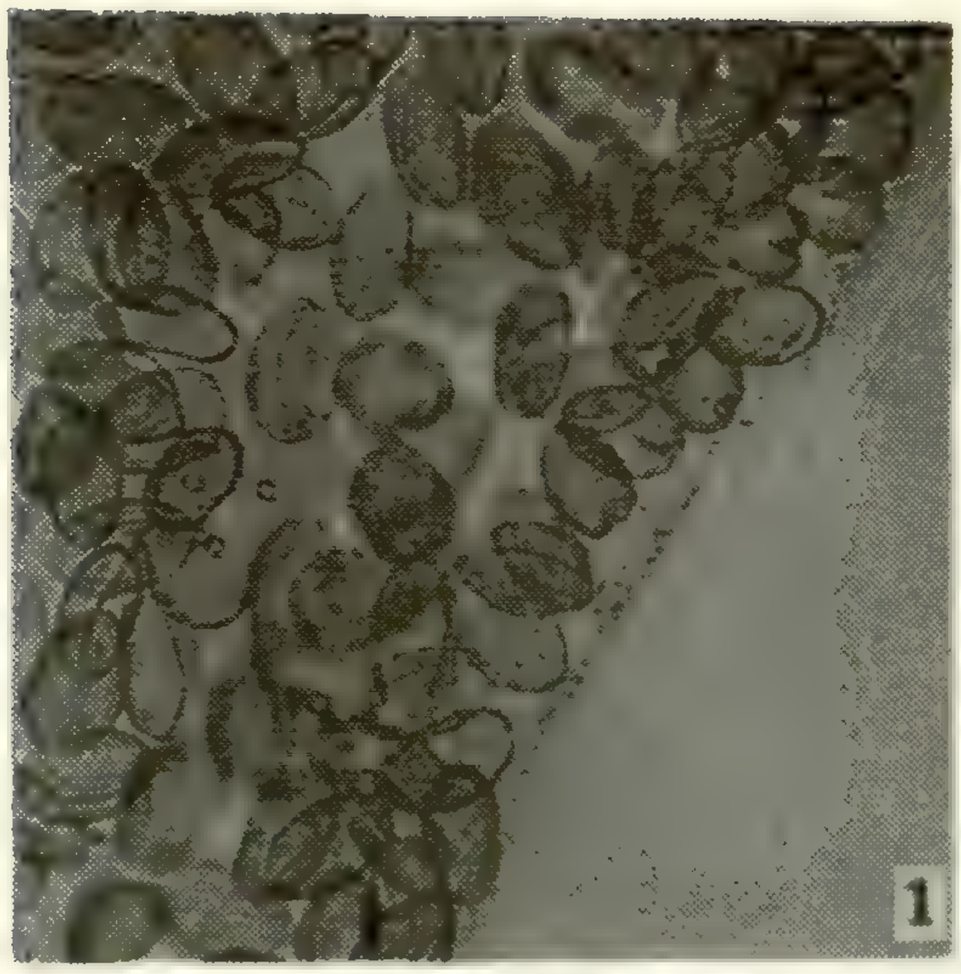
Vander Wyk, R. W. 1950. The comparative morphology of the Annonaceae. (In part, unpublished doctoral thesis, Harvard University, Cambridge, Mass.)
——————— & J. E. Canright. 1956. The anatomy and relationships of the Annonaceae. Trop. Woods **104**:1–24.

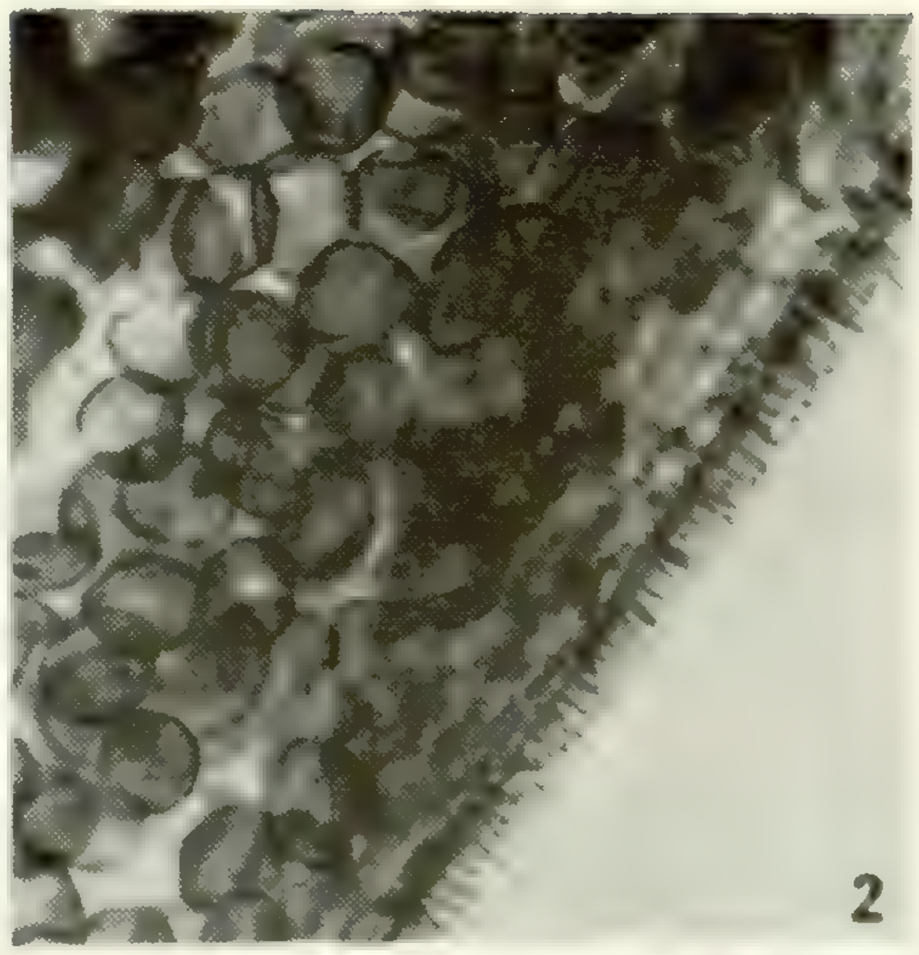
Verdcourt, B. 1969. The status of the genus *Polyalthia* Blume (Annonaceae) in Africa. Adansonia, ser. 2, **9**:87–94.

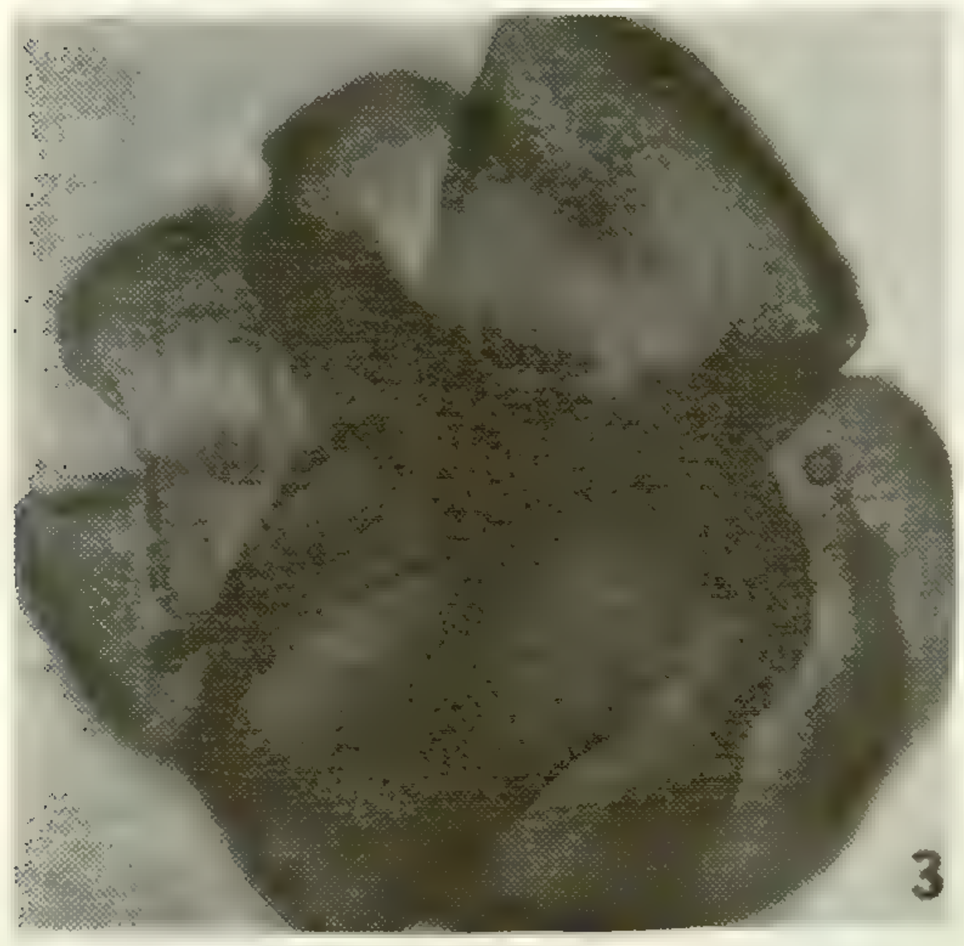
WHITEHEAD, D. R. 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. Evol. **23**:28–35.

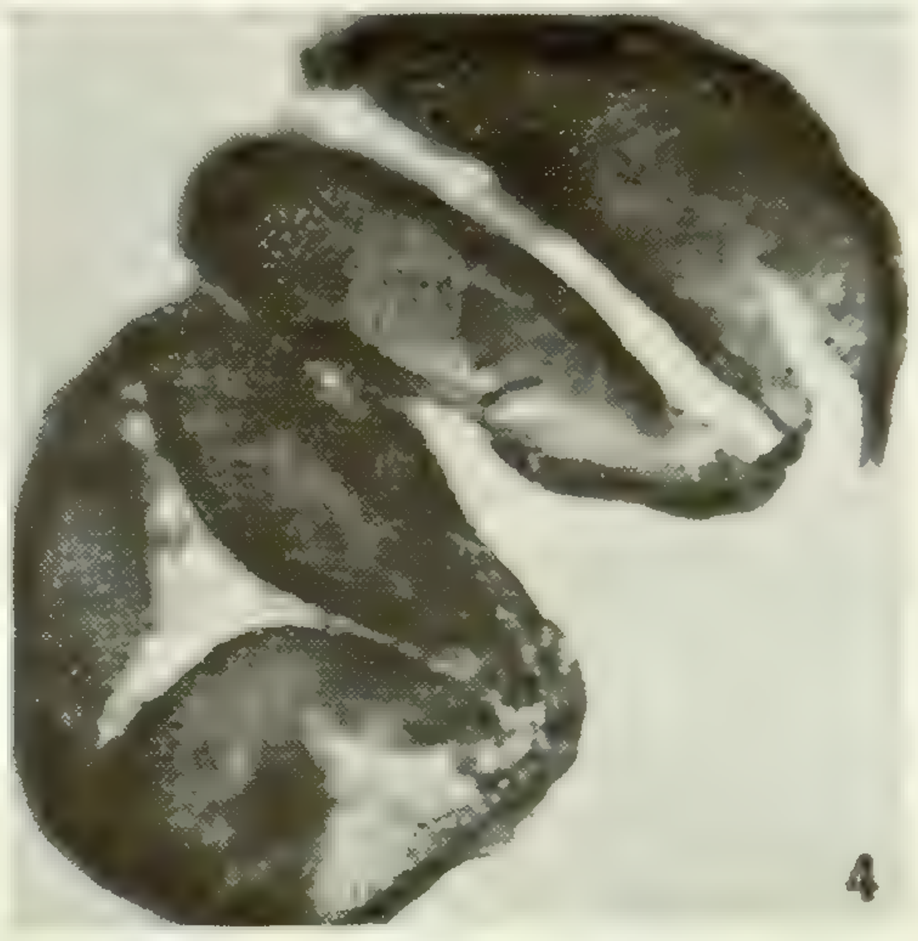
WILSON, T. K. 1964. Comparative morphology of the Canellaceae. III. Pollen. Bot. Gaz. **125**:192–197.

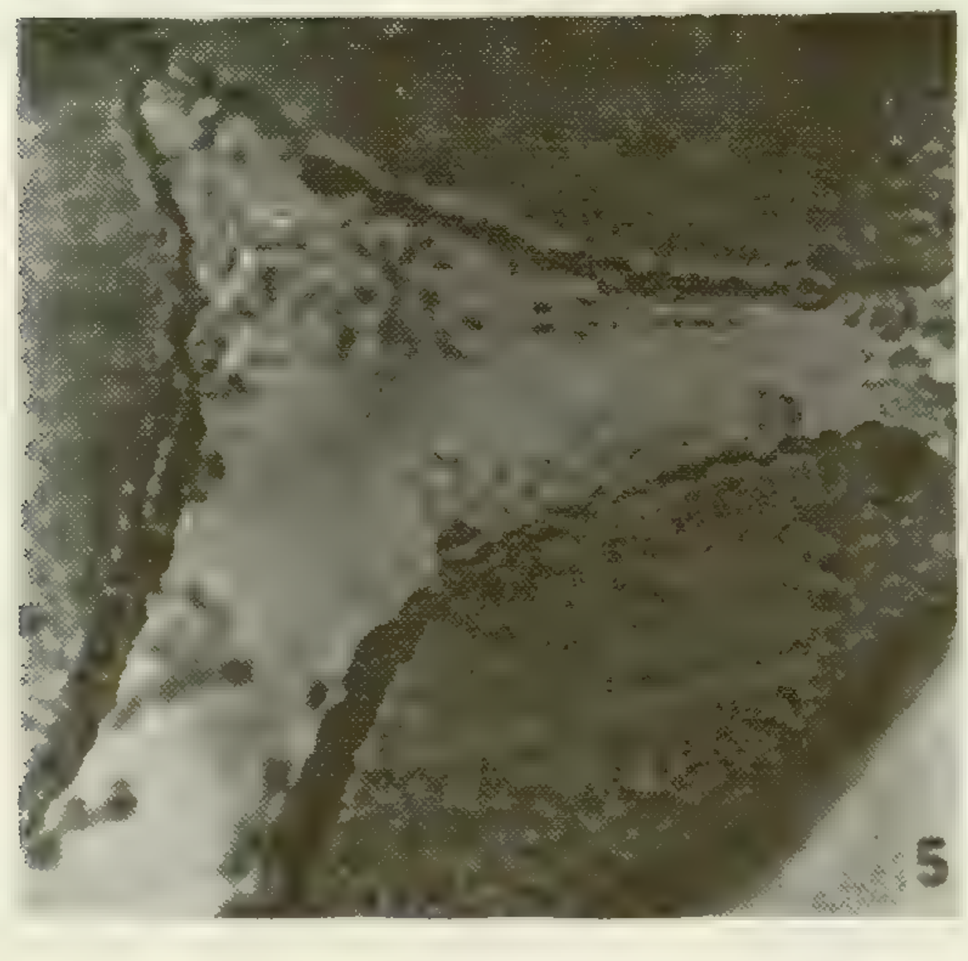
WODEHOUSE, R. P. 1935. Pollen Grains. McGraw-Hill Book Co. (Facsimile of the 1935 edition published by Hafner Publishing Co., New York, 1965.)











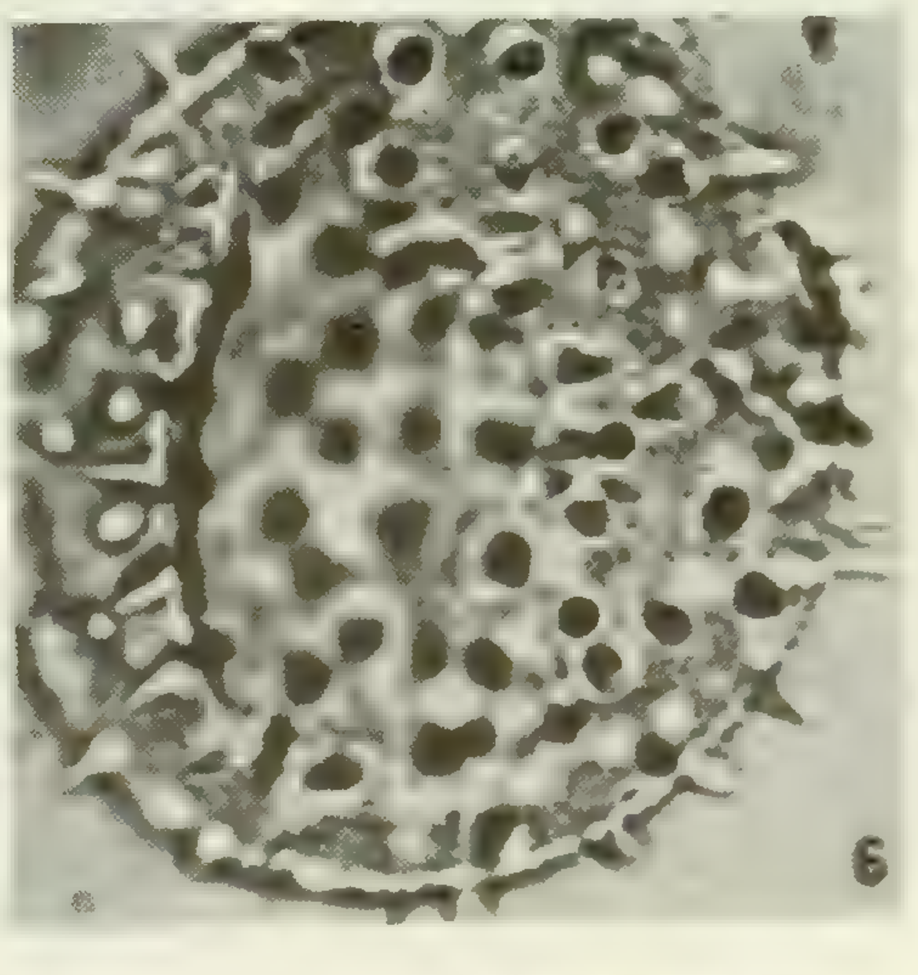
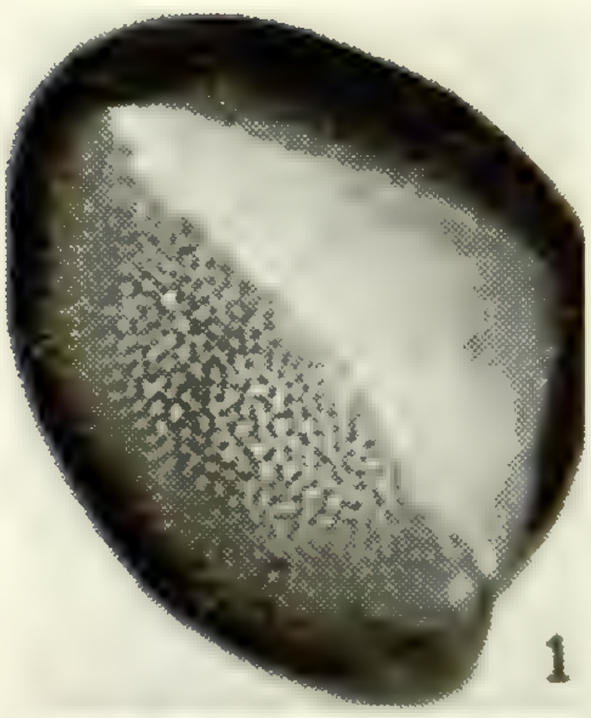
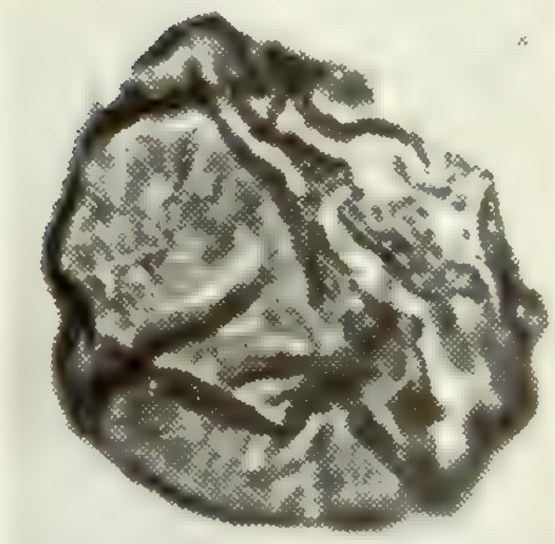
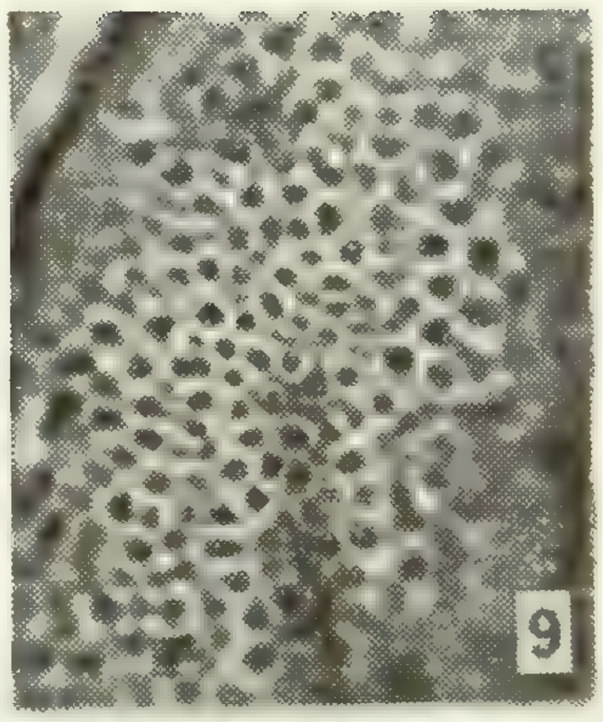
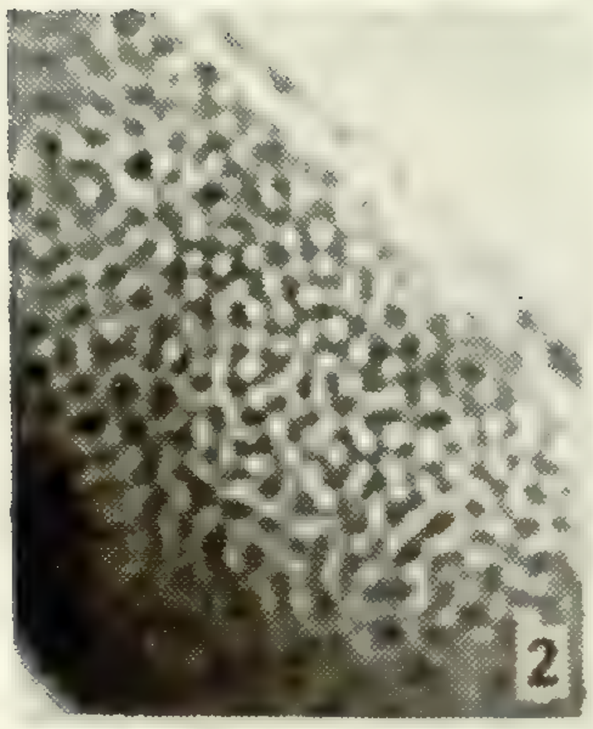


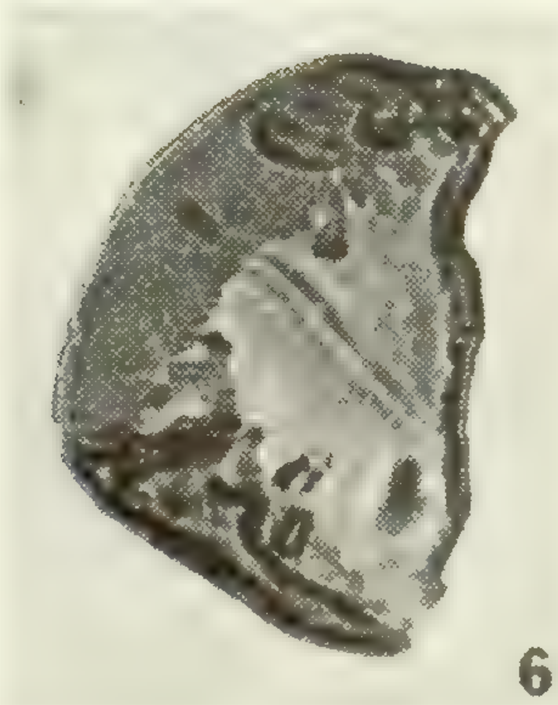
PLATE 1. FIG. 1. *Malmea costaricensis* R. E. Fries, × 200. FIG. 2. *Unonopsis veneficiorum* (Mart.) R. E. Fries, × 200. FIG. 3–5. *Pseudoxandra coriacea* R. E. Fries; Fig. 3,4. × 500; Fig. 5, × 1000. FIG. 6. *Dasymaschalon glaucum* Merr. & Chun. × 1000.

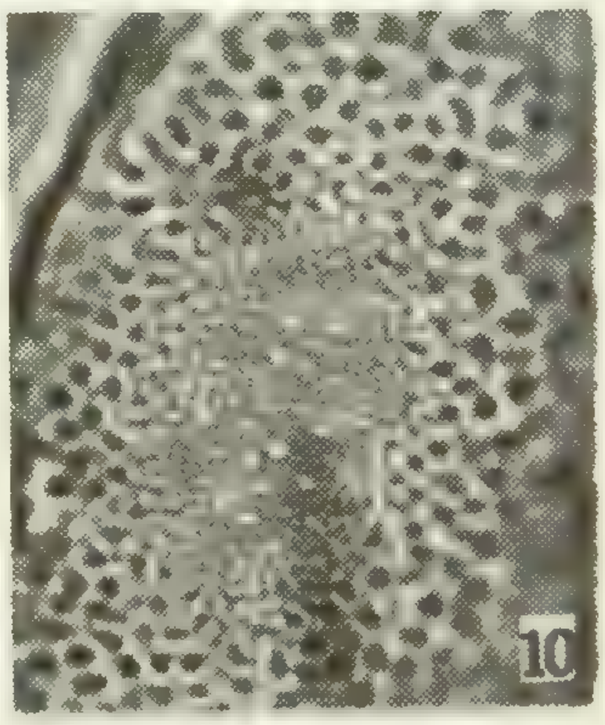


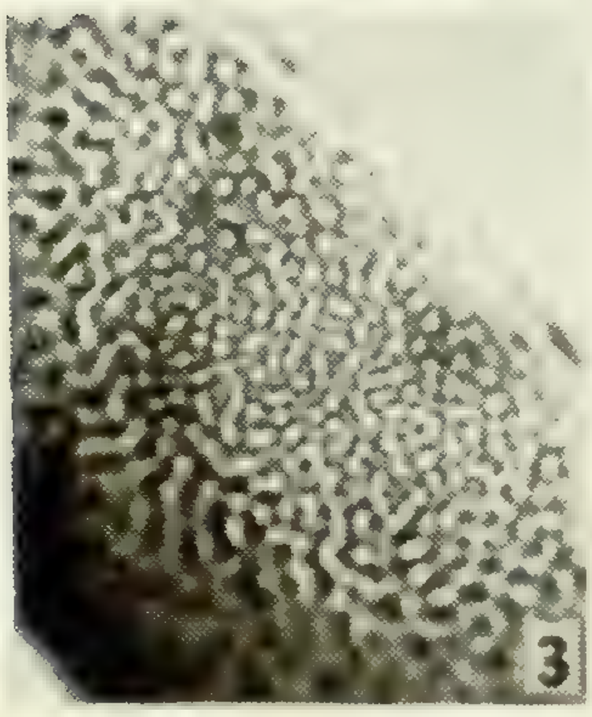


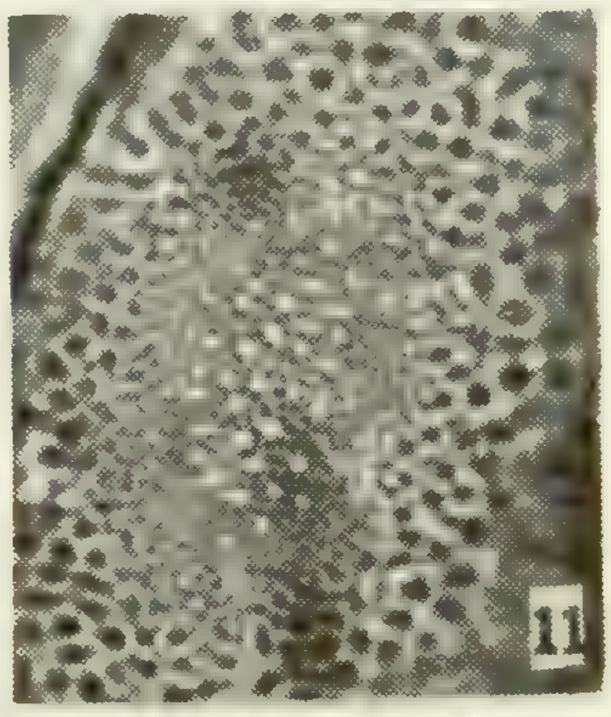












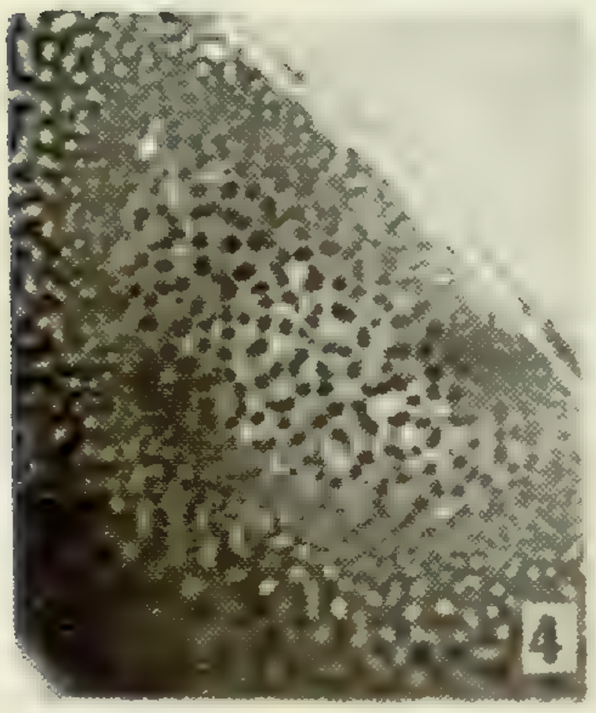
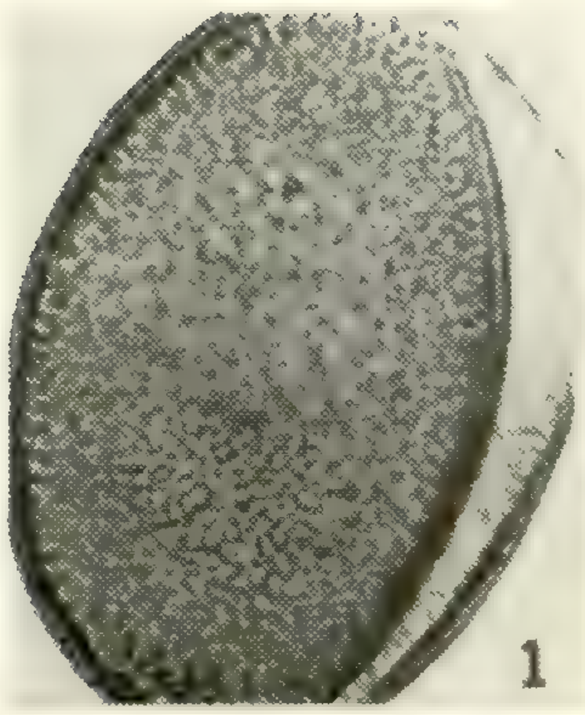
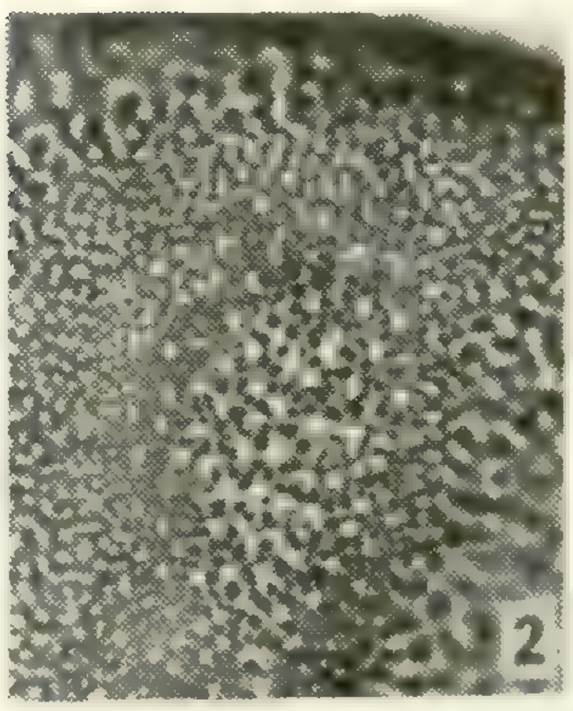
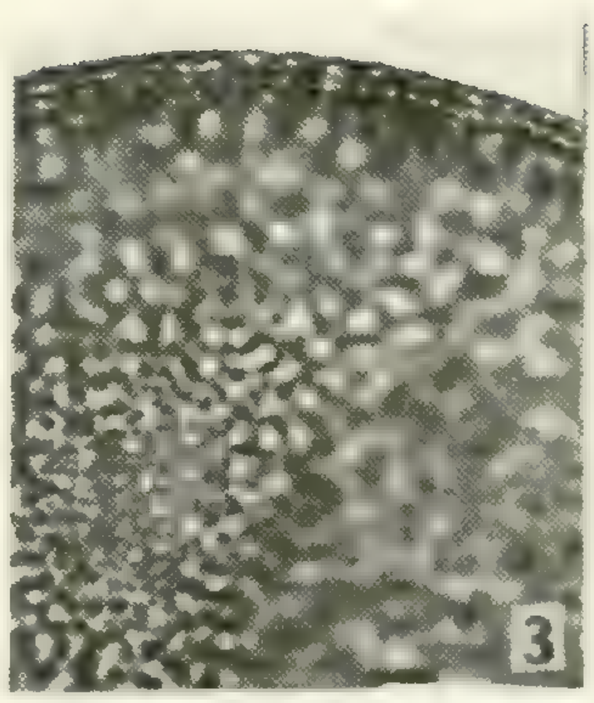
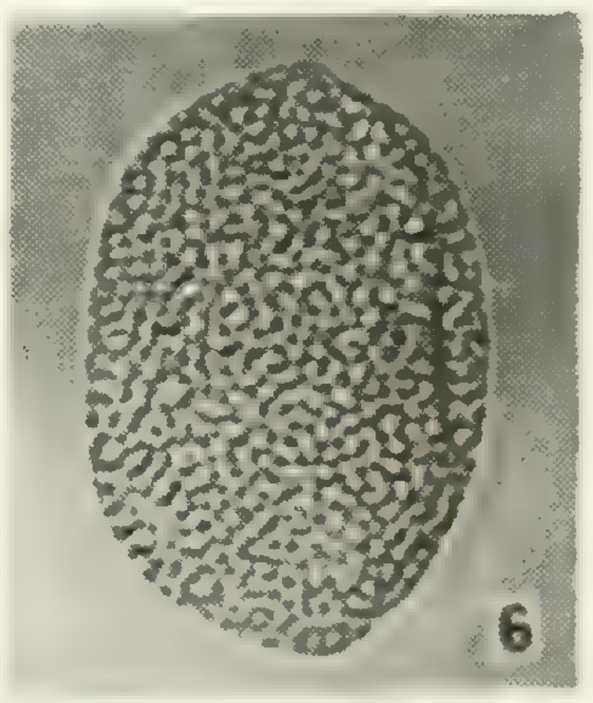


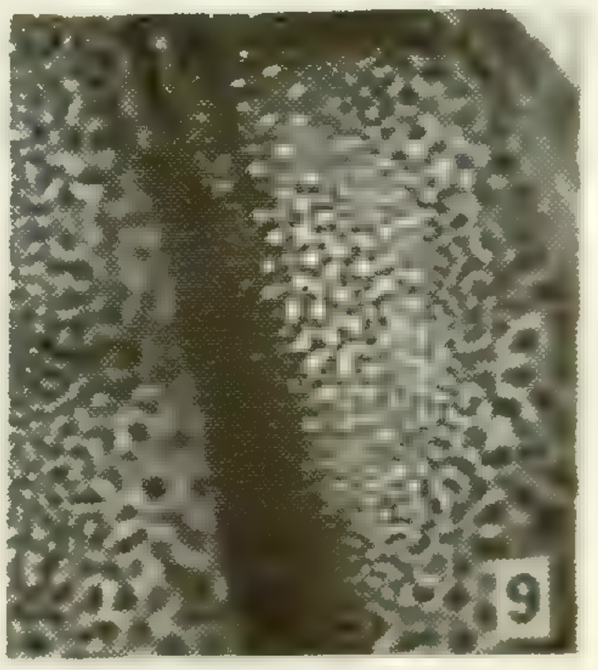
PLATE 2. FIG. 1–4. *Malmea raimondii* (Diels) R. E. Fries; Fig. 1, × 500; Fig. 2–4, × 1000. FIG. 5. *Pseudoxandra polyphleba* (Diels) R. E. Fries, × 500. FIG. 6. *P. williamsii* (R. E. Fries) R. E. Fries, × 500. FIG. 7. *Malmea obovata* R. E. Fries, × 500. FIG. 8–12. *M. costaricensis* R. E. Fries; Fig. 8, × 500; Fig. 9–12, × 1000.

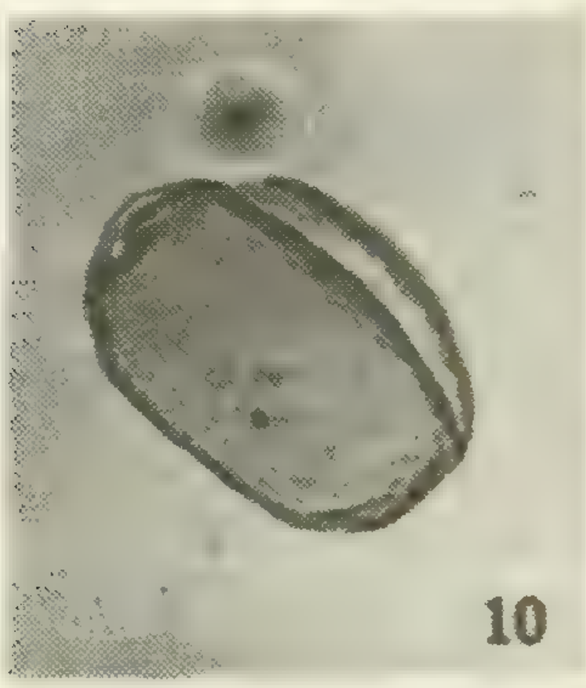


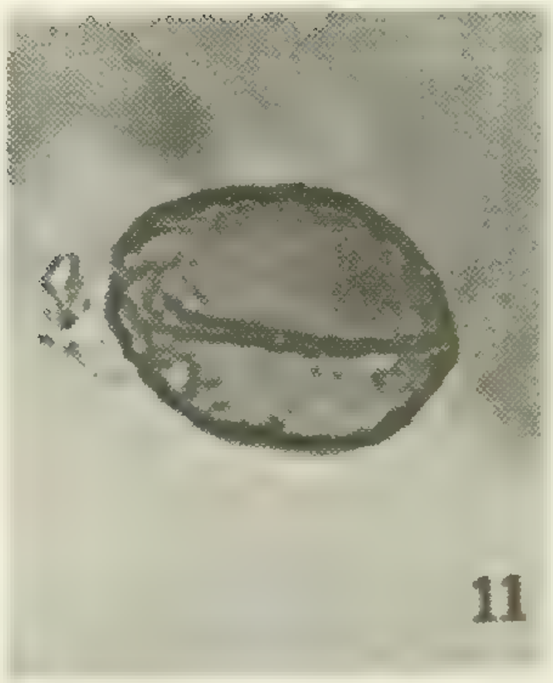












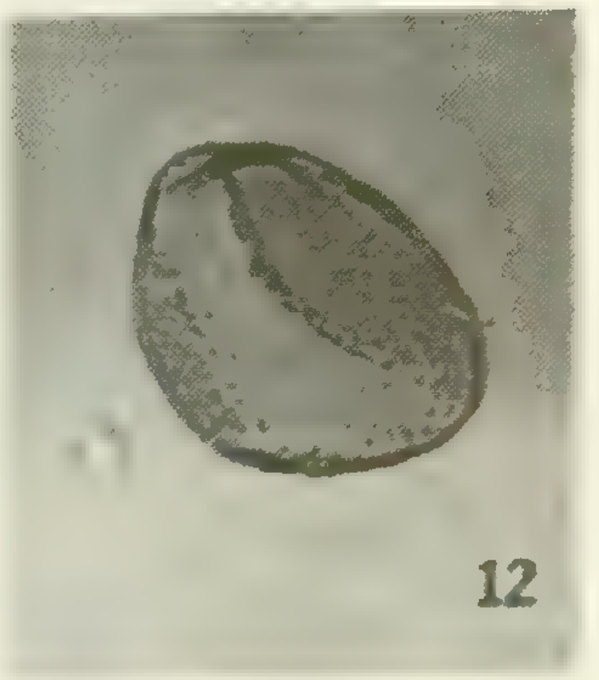
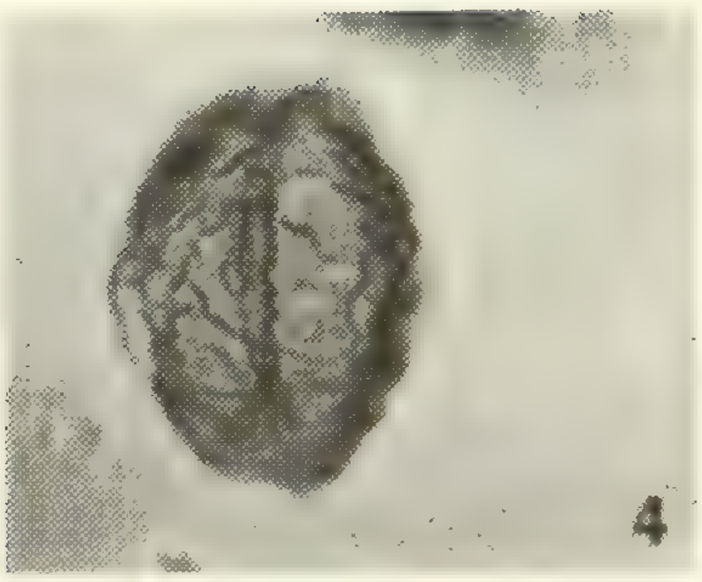
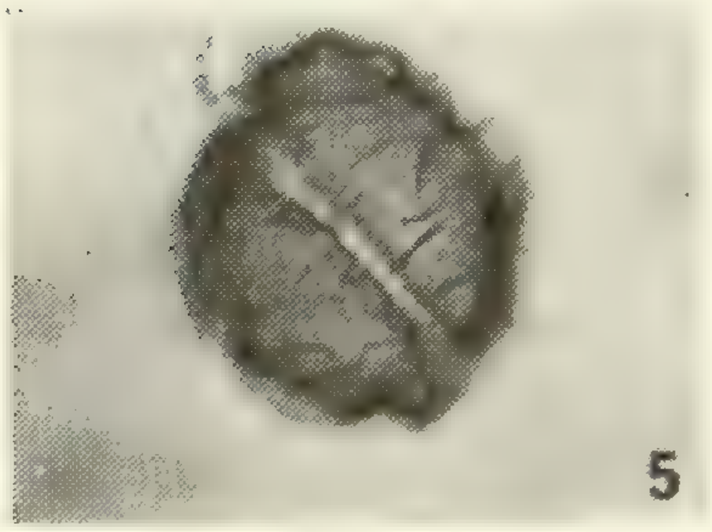


PLATE 3. FIG. 1–3. *Cremastosperma longicuspe* R. E. Fries; Fig. 1, × 500; Fig. 2,3, × 1000. FIG. 4. *C. cauliflorum* R. E. Fries, × 500. FIG. 5. *C. megalophyllum* R. E. Fries, × 500. FIG. 6. *C. anomalum* R. E. Fries, × 500. FIG. 7. *Pseudephedranthus fragrans* (R. E. Fries) Aristeguita × 500. FIG. 8,9. *Ephedranthus guianensis* R. E. Fries; Fig. 8, × 500; Fig. 9, × 1000. FIG. 10. *Oxandra krukoffii* R. E. Fries, × 500. FIG. 11. *O. riedeliana* R. E. Fries, × 500. FIG. 12. *O. laurifolia* (Sw.) A. Rich., × 500.





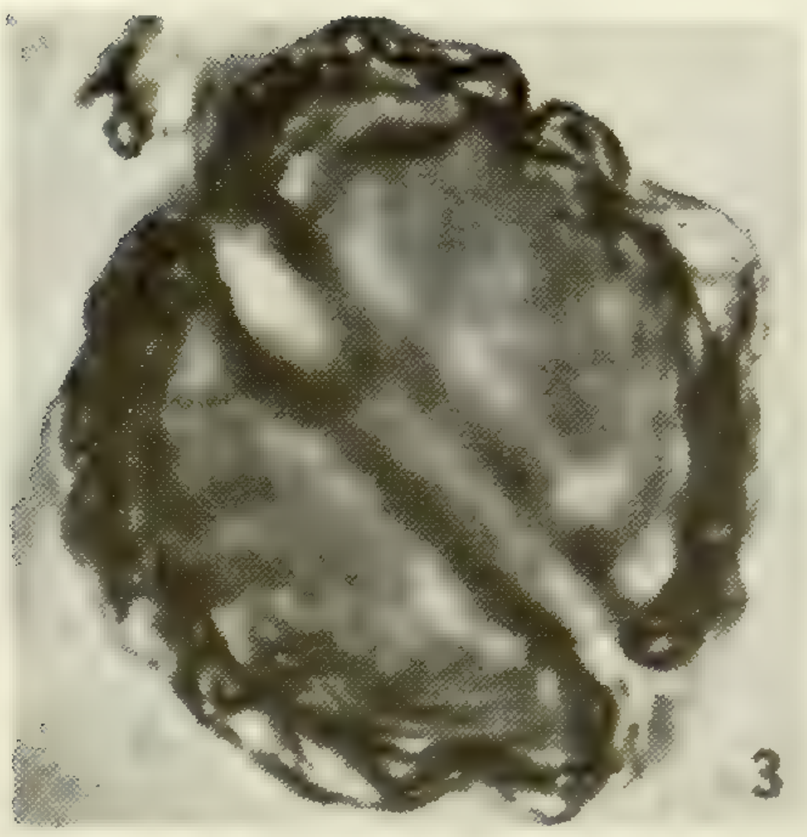
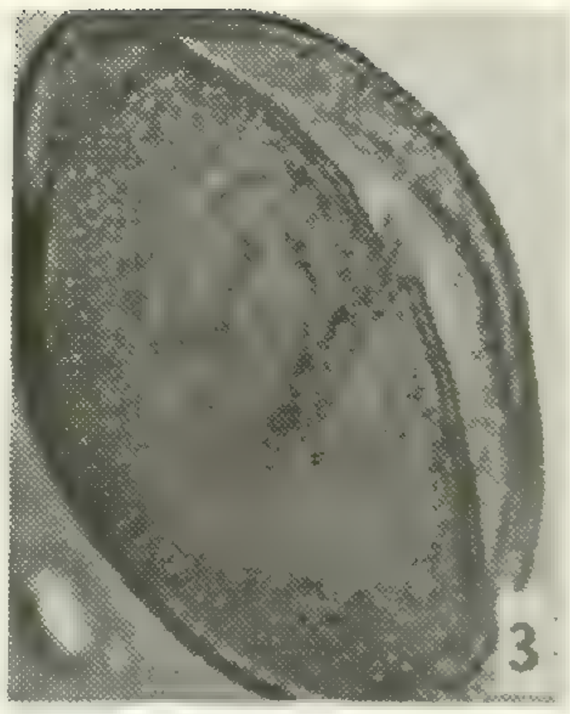
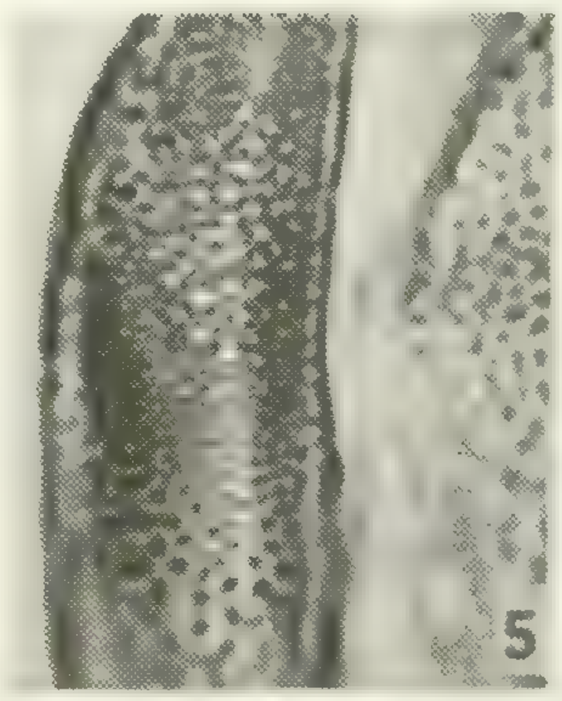
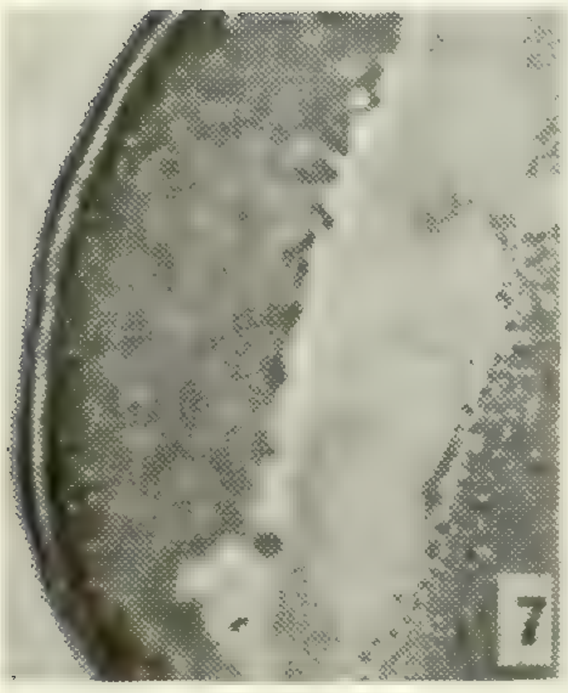
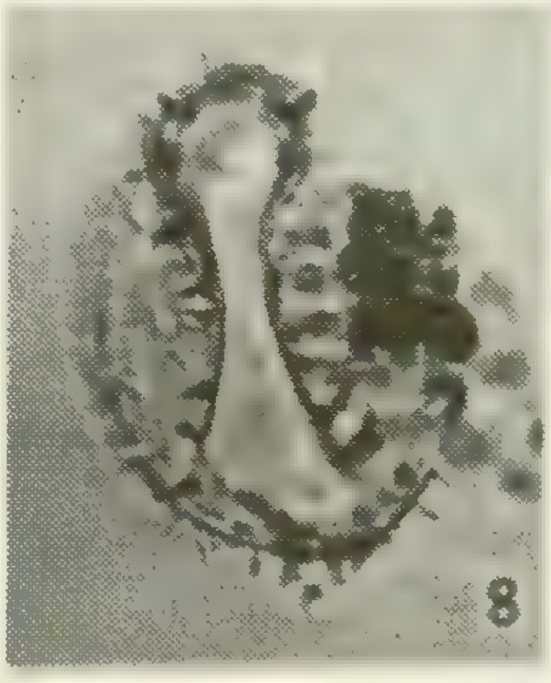


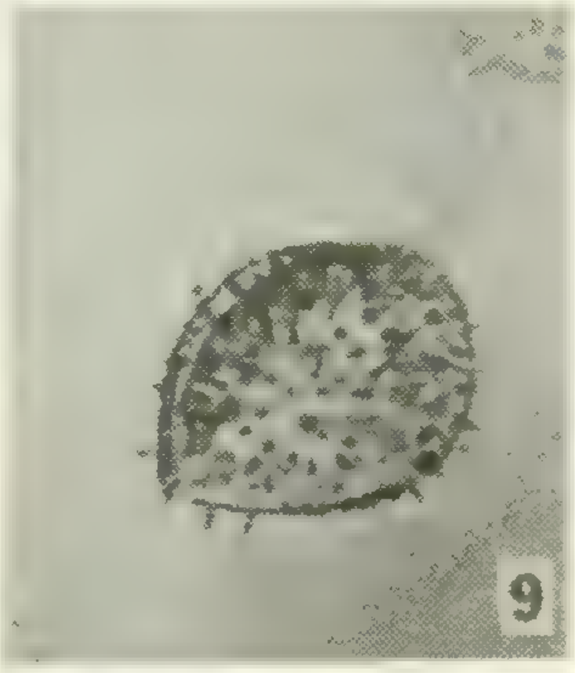
PLATE 4. FIG. 1,4. *Onychopetalum krukoffii* R. E. Fries; Fig. 1, × 1000; Fig. 4, × 500. FIG. 2,3,5. *O. lucidum* R. E. Fries; Fig. 2,3, × 1000; Fig. 5, × 500. FIG. 6. *Bocageopsis multiflora* (Mart.) R. E. Fries, × 500. FIG. 7. *Ruizodendron ovale* (Ruiz & Pav.) R. E. Fries, × 1000.

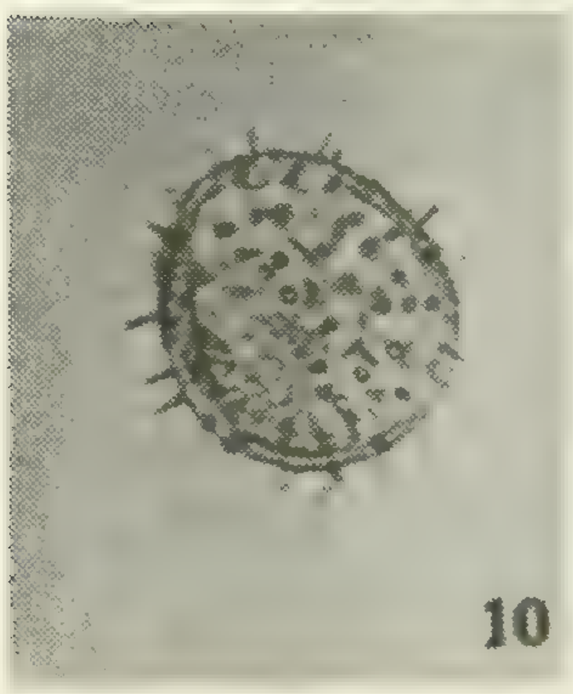


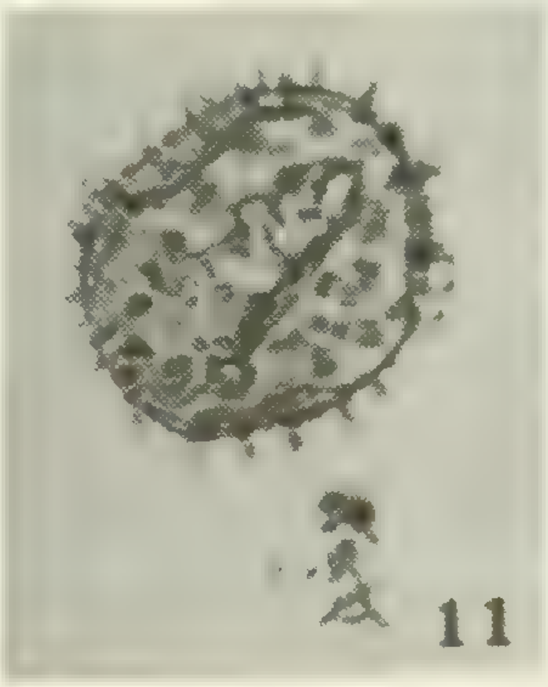












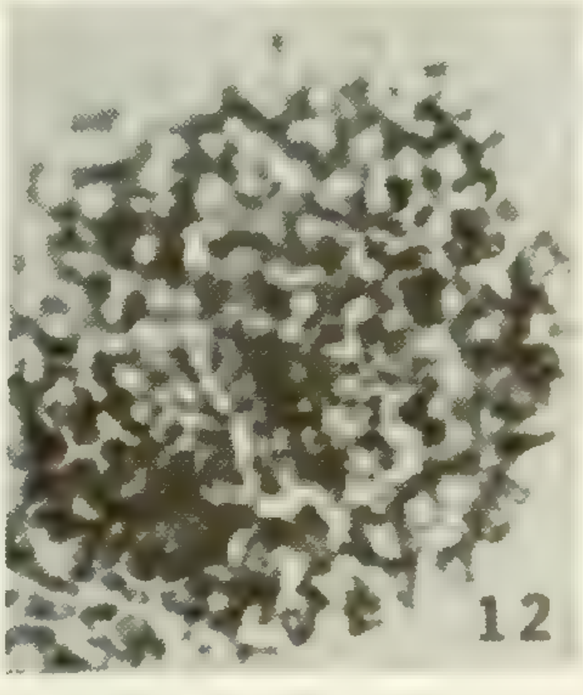
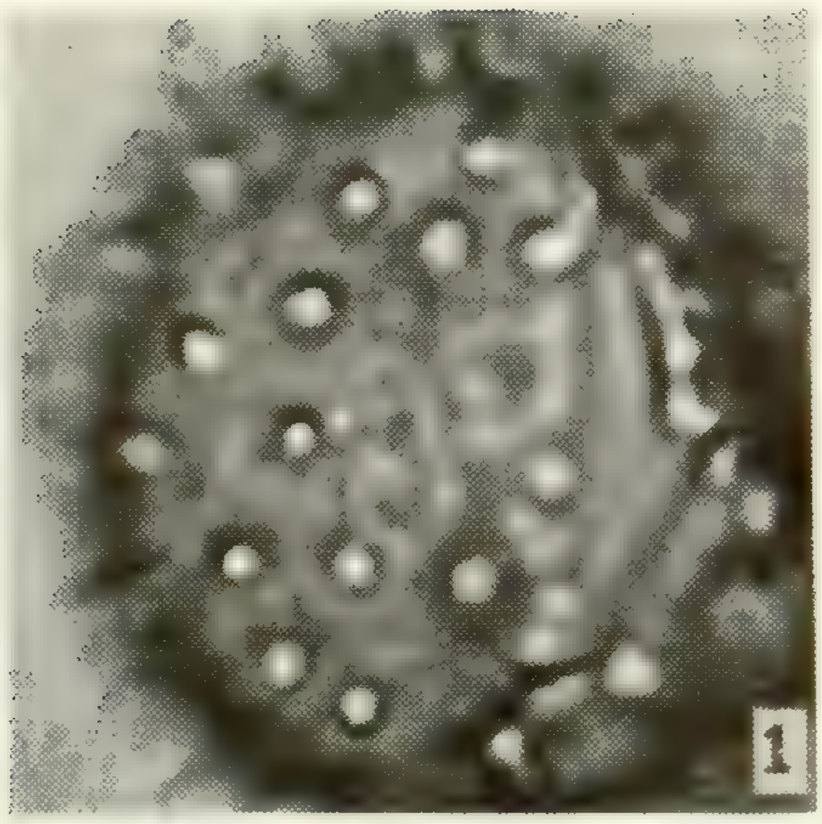
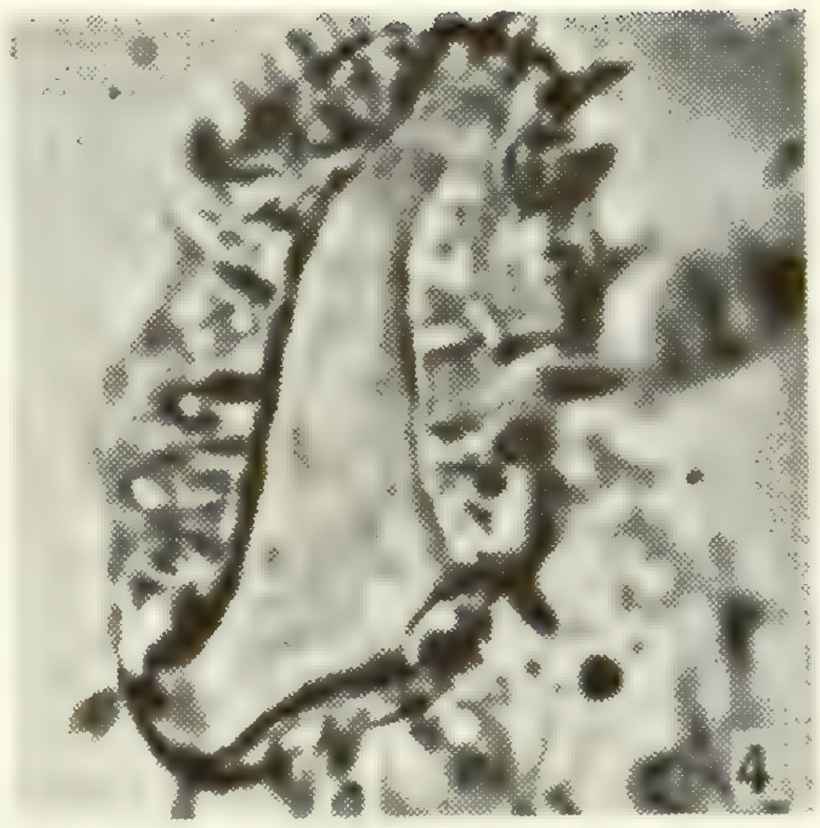
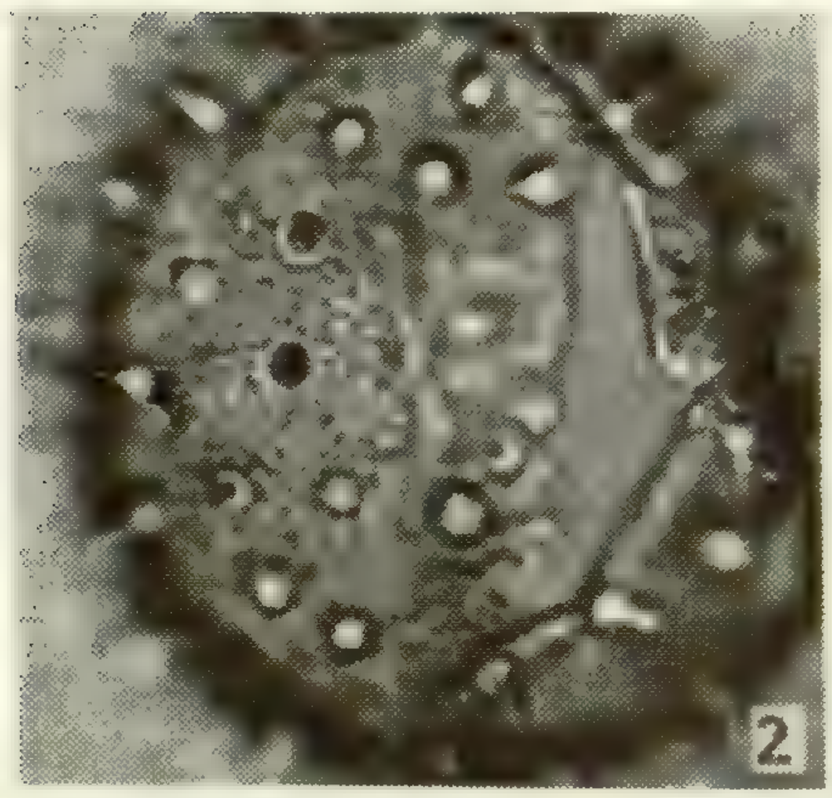
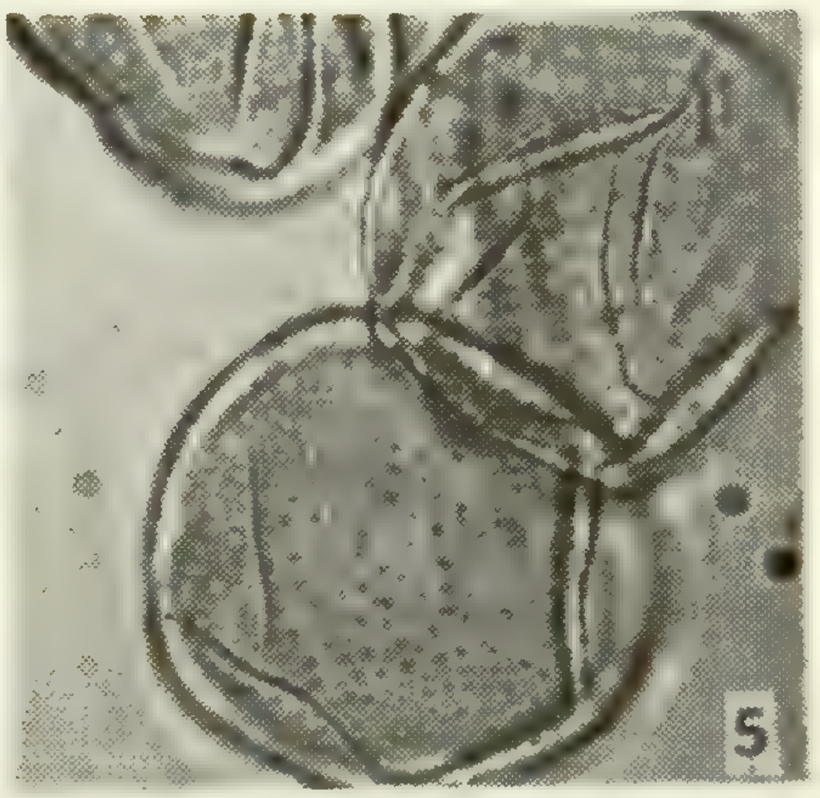


PLATE 5. FIG. 1. *Unonopsis glaucopetala* R. E. Fries, × 500. FIG. 2. *U. grandis* (Benth.) R. E. Fries, × 500. FIG. 3. *Monocarpia marginalis* (Scheff.) J. Sincl., × 500. FIG. 4,5. *Enantia kummeriae* Engl. & Diels; Fig. 4, × 500; Fig. 5, × 1000. FIG. 6,7. *Polyceratocarpus parviflorus* (Bak.f.) Ghesq.; Fig. 6, × 500; Fig. 7, × 1000. FIG. 8. *Desmos cochinchinensis* Lour., × 500. FIG. 9. *D. lawii* (Hk.f. & Th.) Saff., × 500. FIG. 10. *D. dunalii* (Wall. ex Hk.f. & Th.) Saff., × 500. FIG. 11. *D. zeylanicus* (Hk.f. & Th.) Saff., × 500. FIG. 12. *Dasymaschalon clusiflorum* (Merr.) Merr., × 1000.









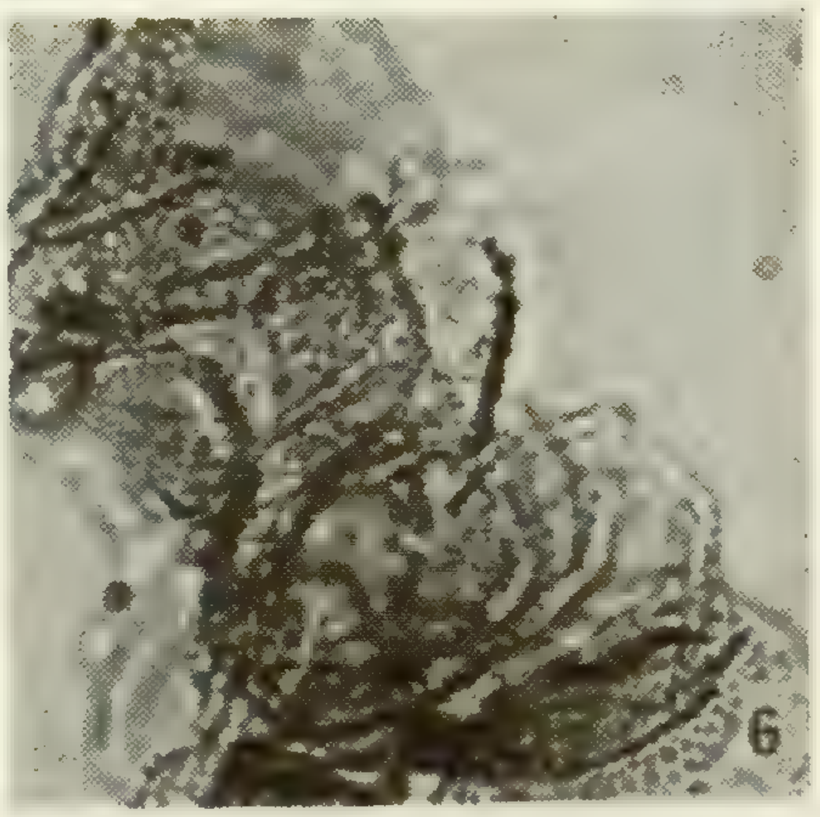
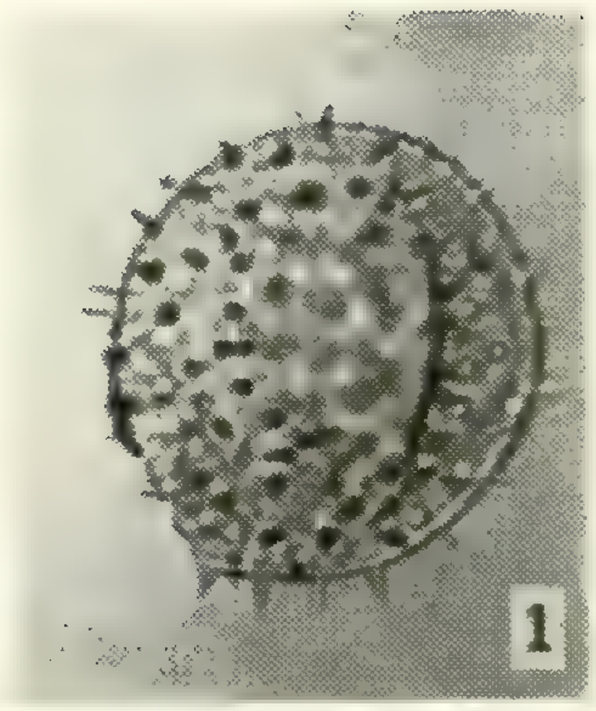
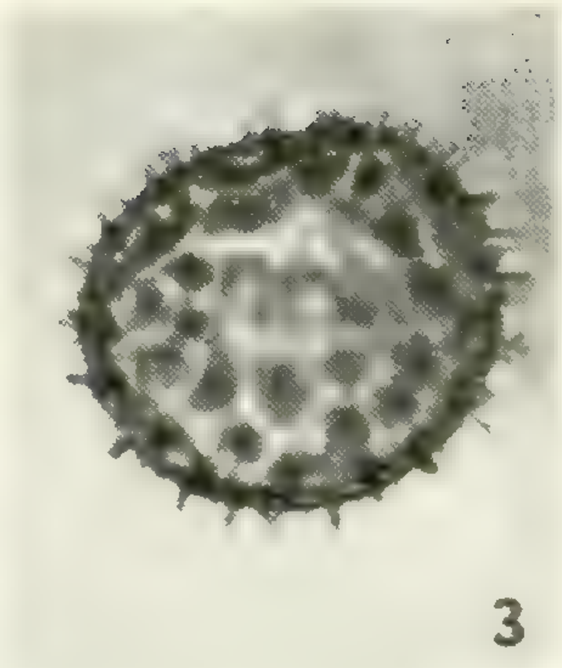
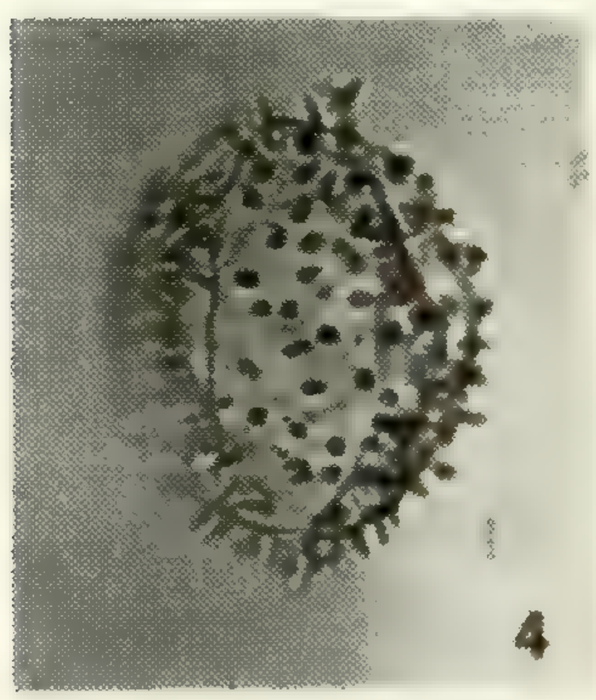
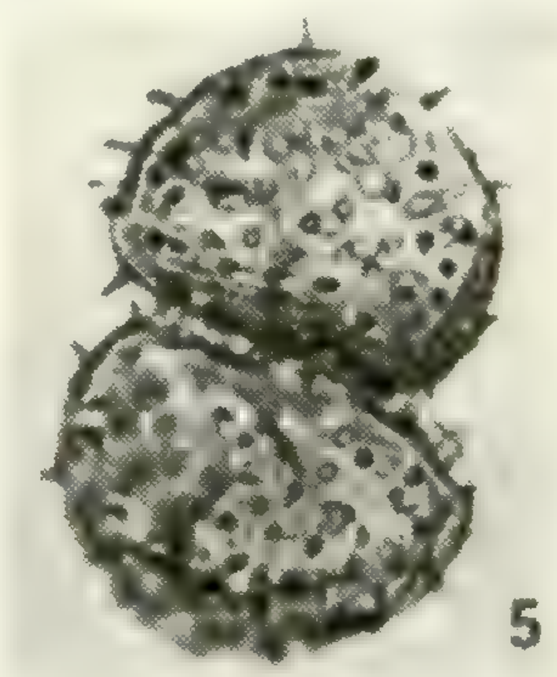


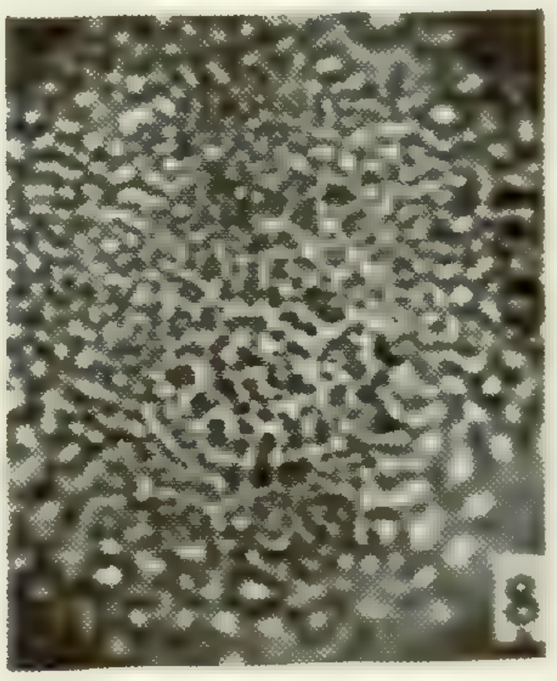
PLATE 6. FIG. 1–3. *Dasymaschalon sootepense* Craib, × 1000. FIG. 4. *Desmos dumosus* (Roxb.) Saff., × 1000. FIG. 5. *Monanthotaxis poggei* Engl. & Diels, × 1000. FIG. 6. *Enneastemon mannii* (Baill.) Keay, × 1000.

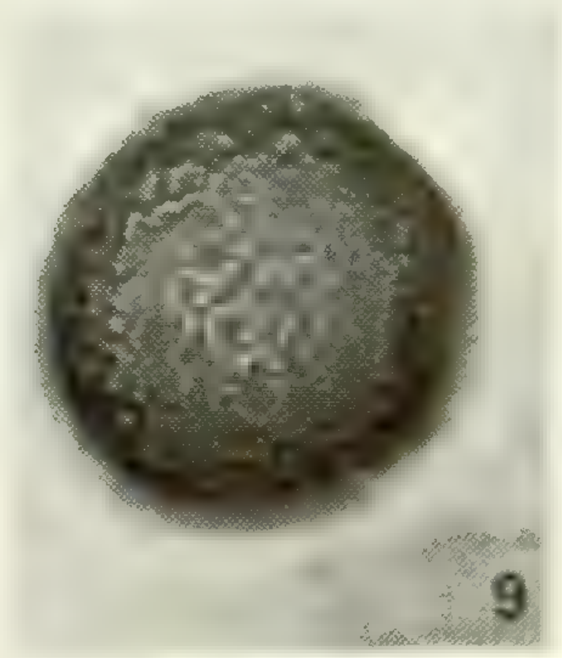


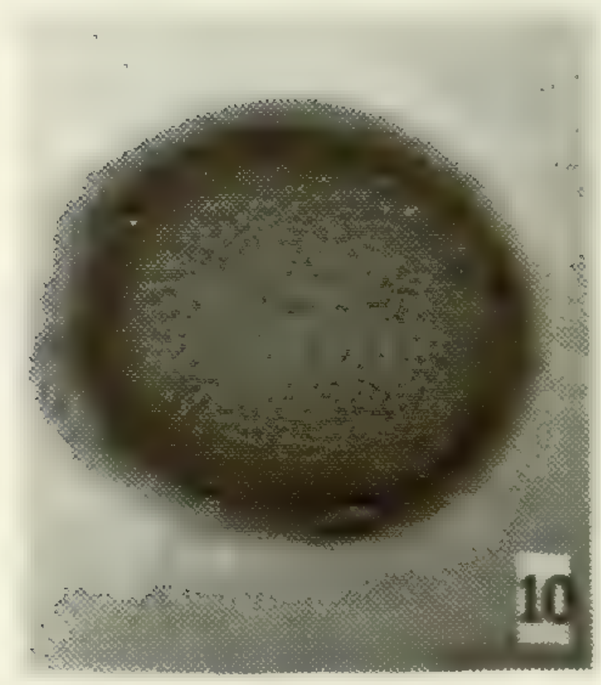












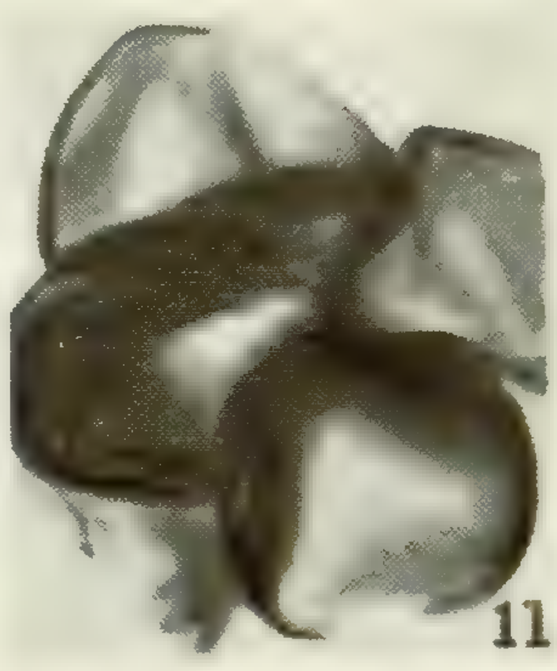
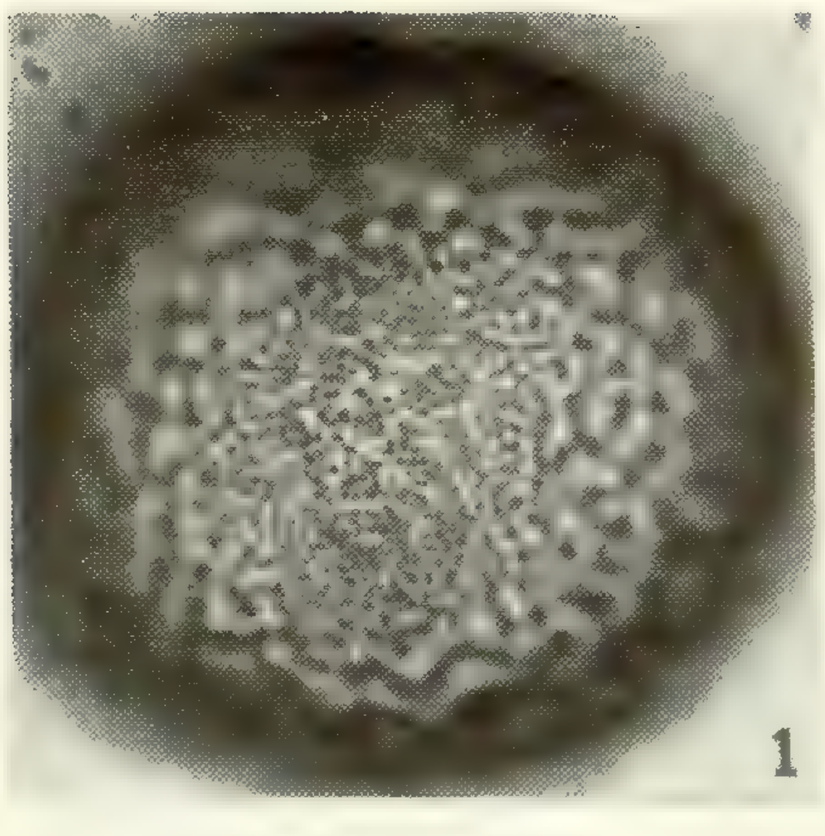
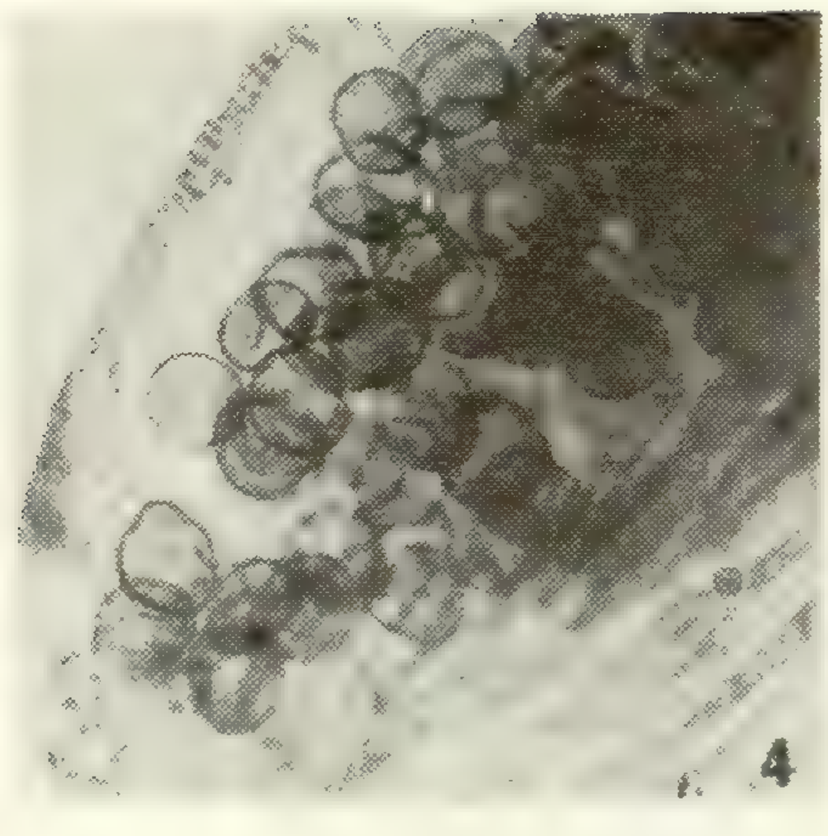
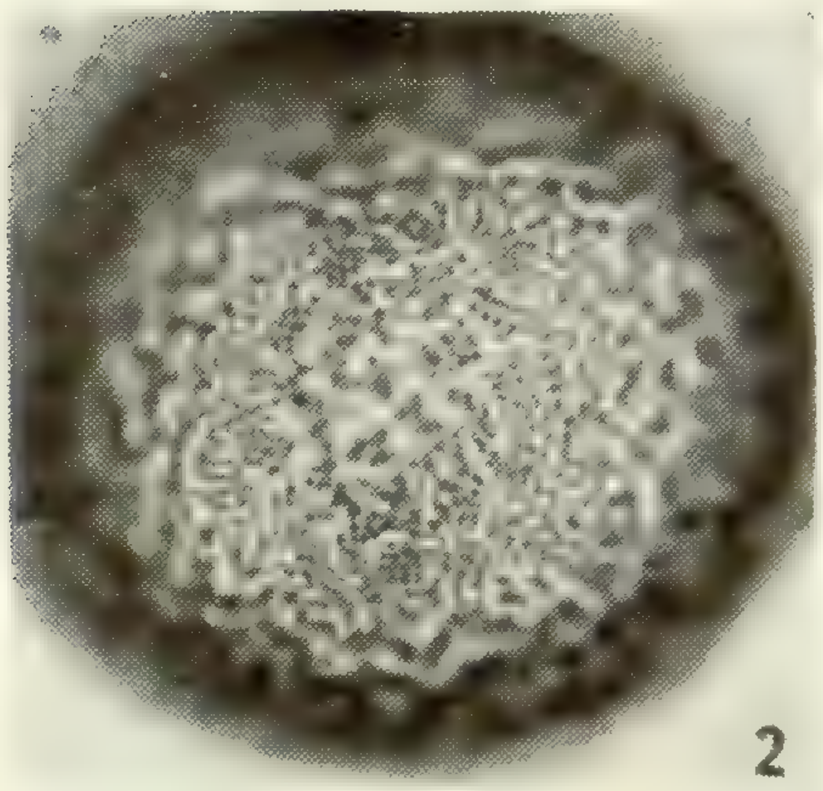
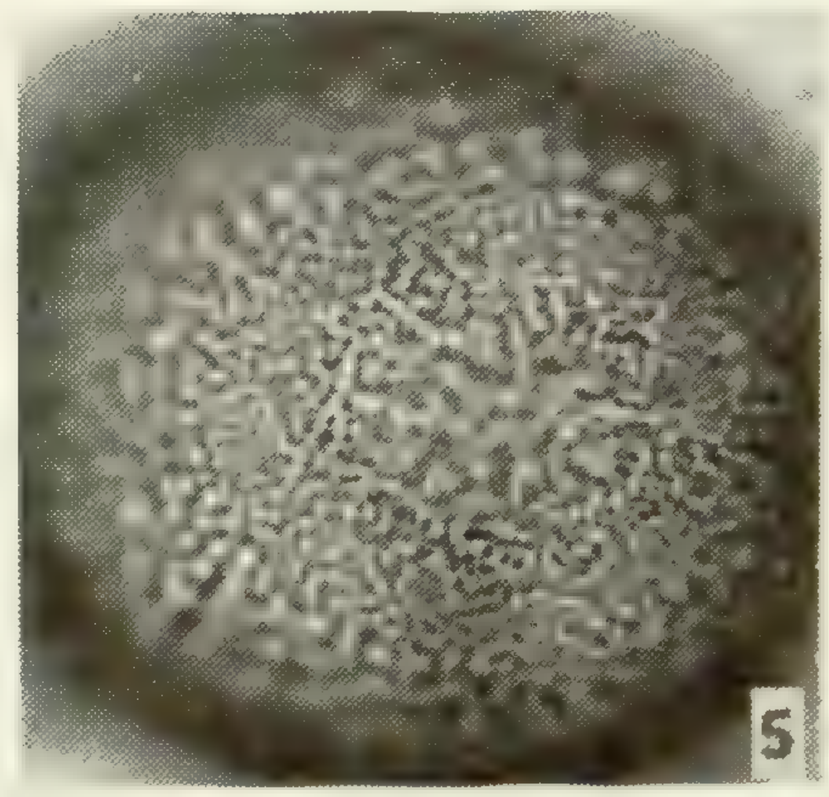


PLATE 7. FIG. 1. *Dasymaschalon glaucum* Merr. & Chun, × 500. FIG. 2,3. *D. sootepense* Craib, × 500. FIG. 4. *Friesodielsia beccarii* (Diels) van Steenis, × 500. FIG. 5. *F. bakeri* (Merr.) van Steenis, × 500. FIG. 6. *Enneastemon foliosus* (Engl. & Diels) Robyns & Ghesq., × 1000. FIG. 7. *Stenanona panamensis* Standl., × 500. FIG. 8. *S. costaricensis* R. E. Fries, × 1000. FIG. 9. *Reedrollinsia* Walker, × 500. FIG. 10. *Desmopsis panamensis* (Robinson) Saff., × 500. FIG. 11. *Tetrameranthus macrocarpus* R. E. Fries, × 500. FIG. 12. *Duguetia stelechantha* (Diels) R. E. Fries, × 500.









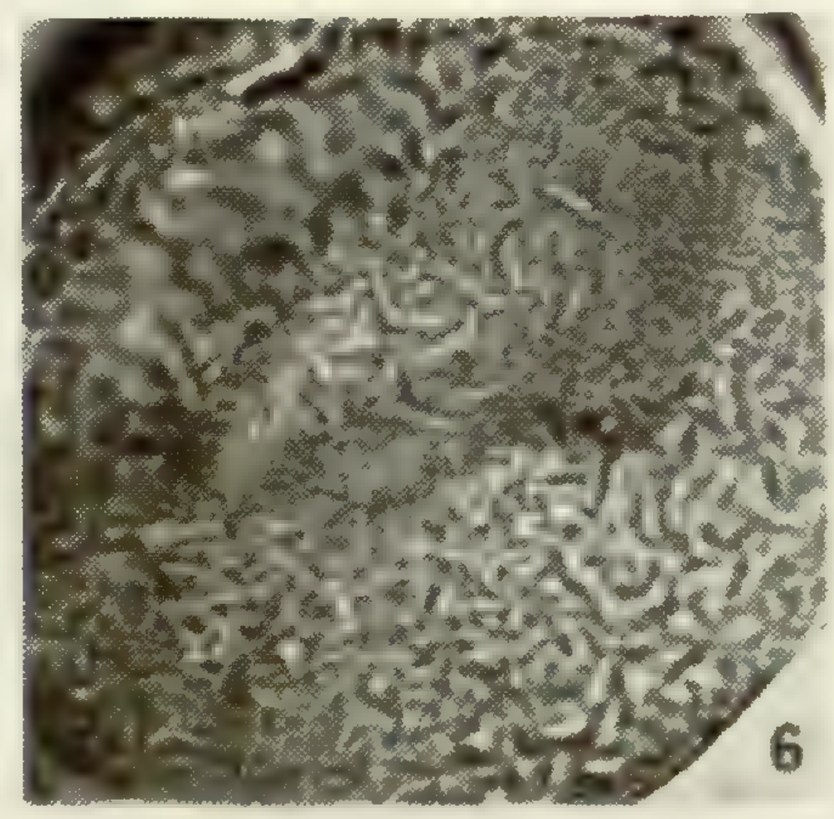
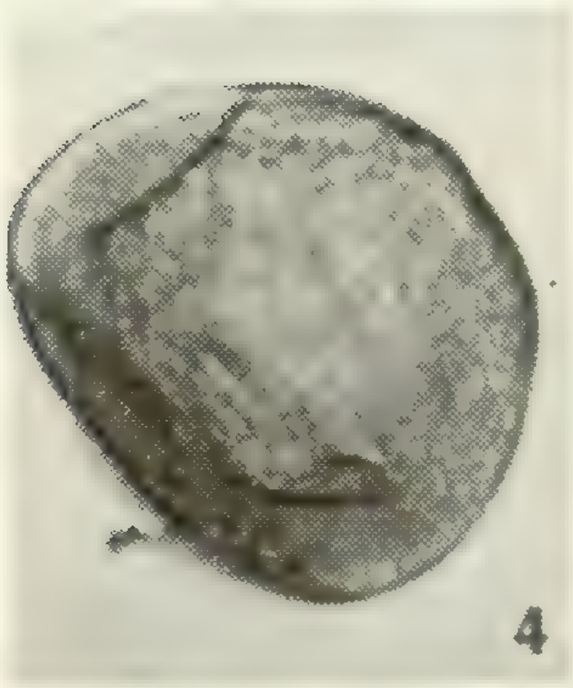
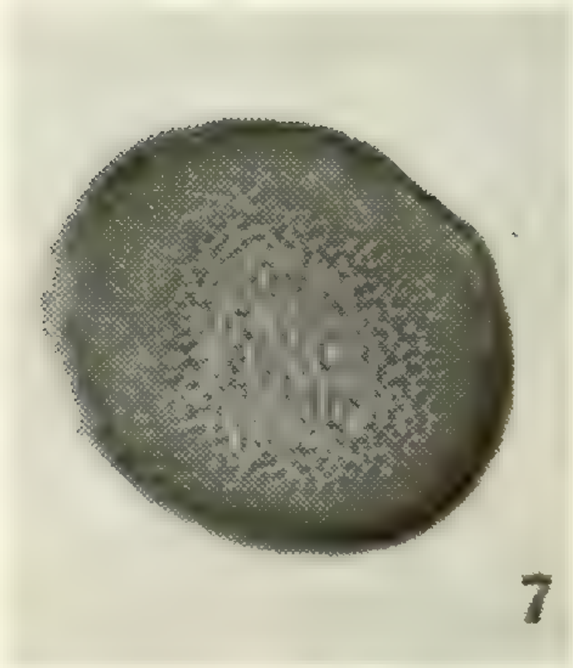
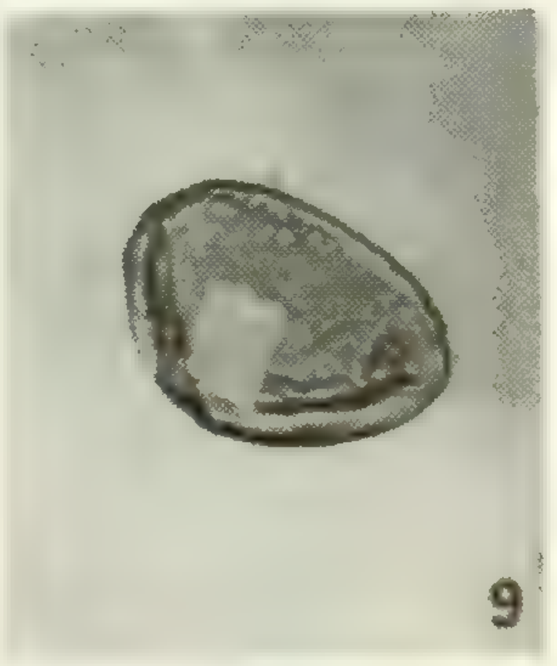
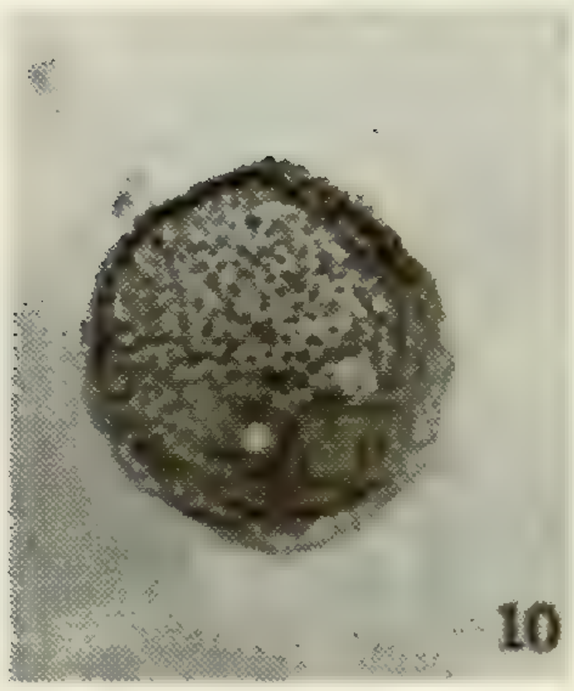


PLATE 8. FIG. 1–3. *Reedrollinsia* Walker, × 1000. FIG. 4,5. *Desmopsis panamensis* (Robinson) Saff., Fig. 4. × 200; Fig. 5, × 1000. FIG. 6. *Uvaria javana* Dunal, × 1000.









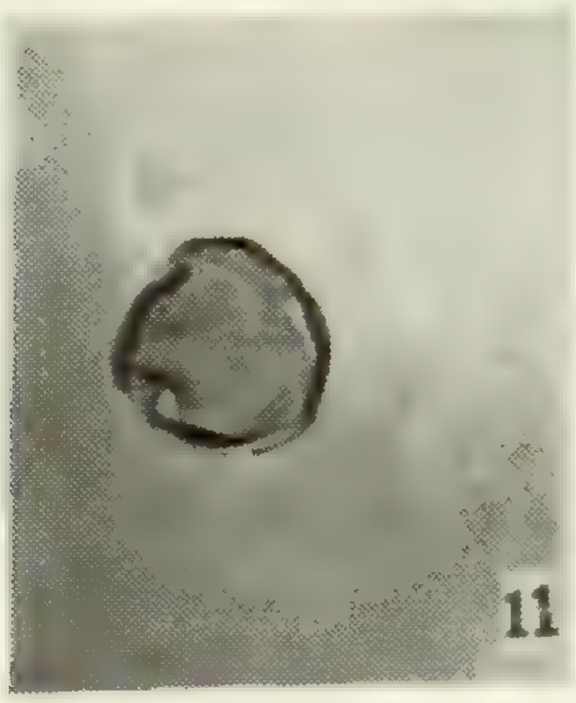
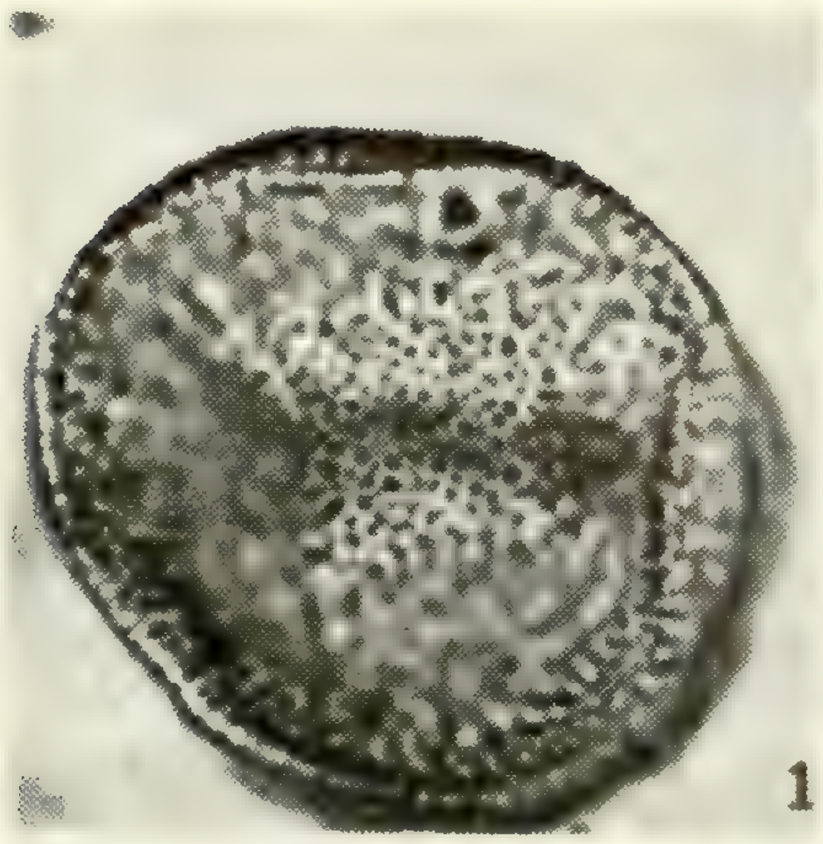
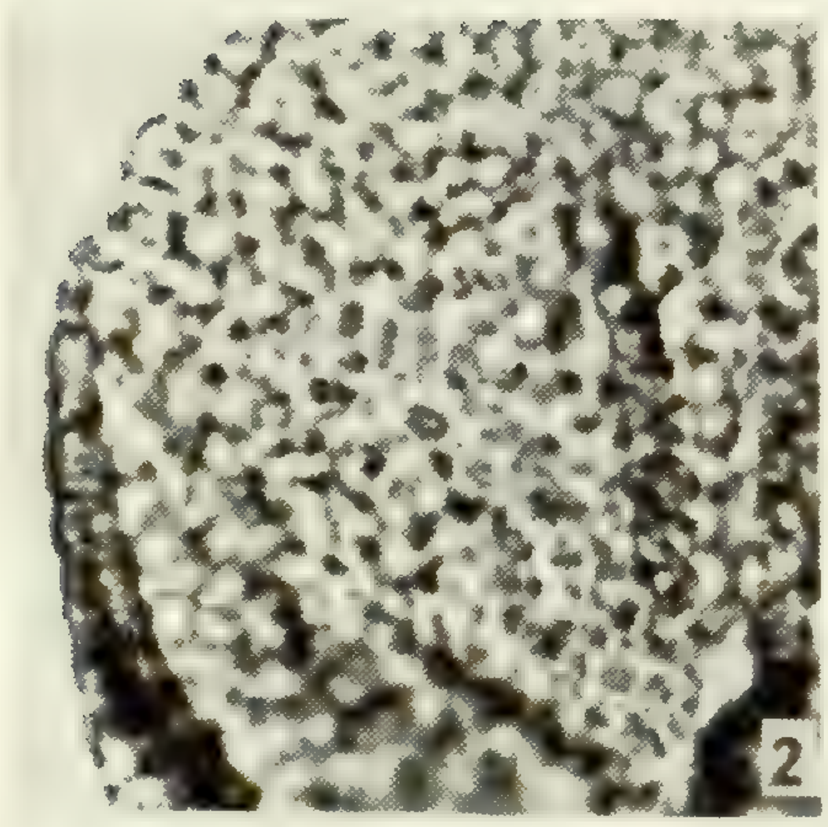


PLATE 9. FIG. 1. *Uvaria bipindensis* Engl., × 500. FIG. 2. *U. purpurea* Bl., × 1000. FIG. 3. *Anomianthus dulcis* (Dunal) J. Sincl., × 500. FIG. 4. *Tetrapetalum borneense* Merr., × 500. FIG. 5. *Ellipeia cuneifolia* Hk.f. & Th., × 500. FIG. 6. *Cyathostemma excelsum* (Hk.f. & Th.) J. Sincl., × 500. FIG. 7,8. *Enicosanthum grandifolium* (Elmer) Airy-Shaw; Fig. 7, × 500; Fig. 8, × 1000. FIG. 9. *Cleistopholis patens* (Benth.) Engl. & Diels, × 500. FIG. 10. *Sageraea thwaitesii* Hk.f. & Th., × 500. FIG. 11. *Stelechocarpus burahol* (Bl.) Hk.f. & Th., × 500. FIG. 12. *Alphonsea lutea* (Roxb.) Hk.f. & Th., × 500.





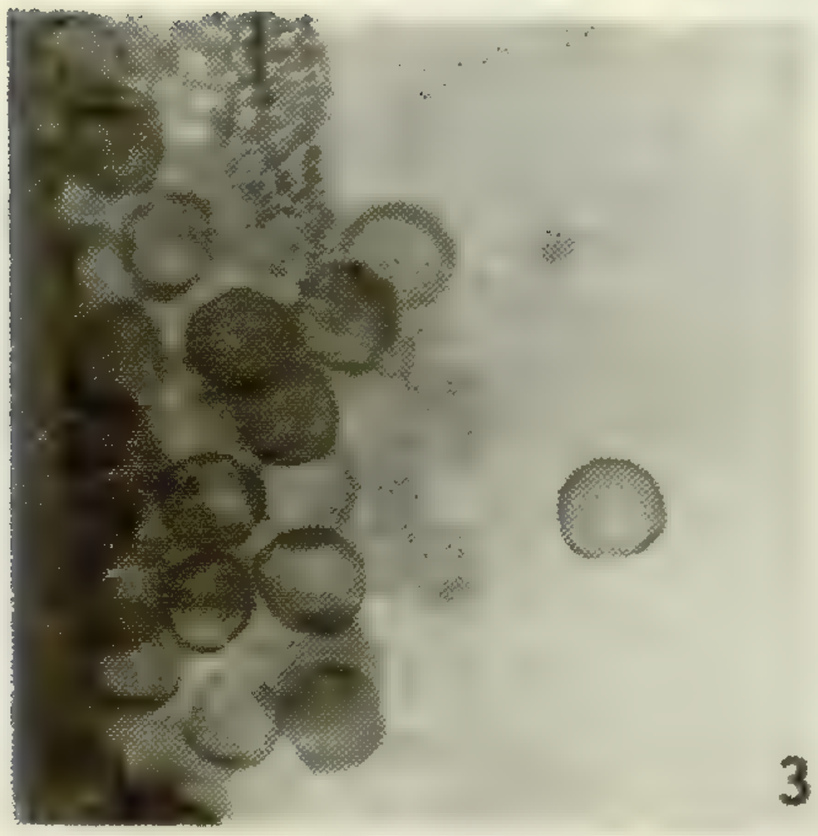
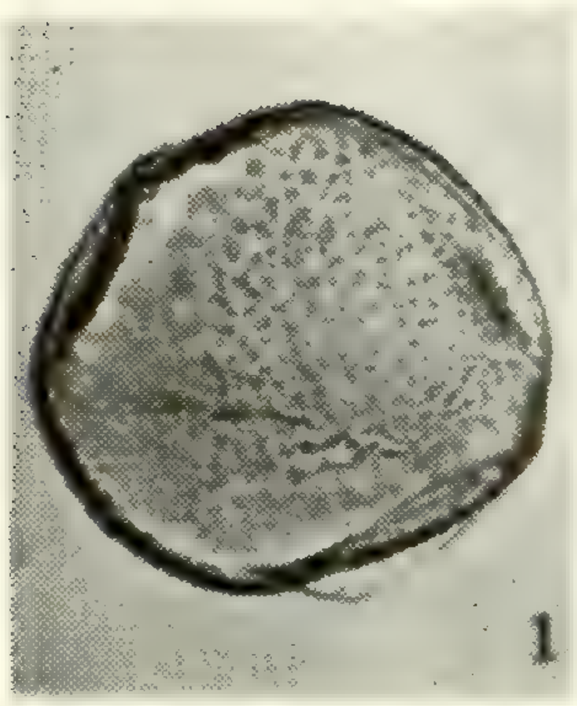
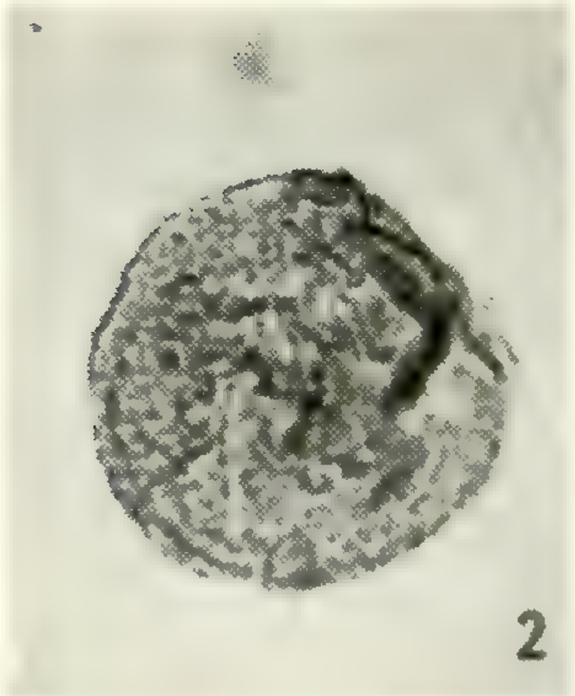
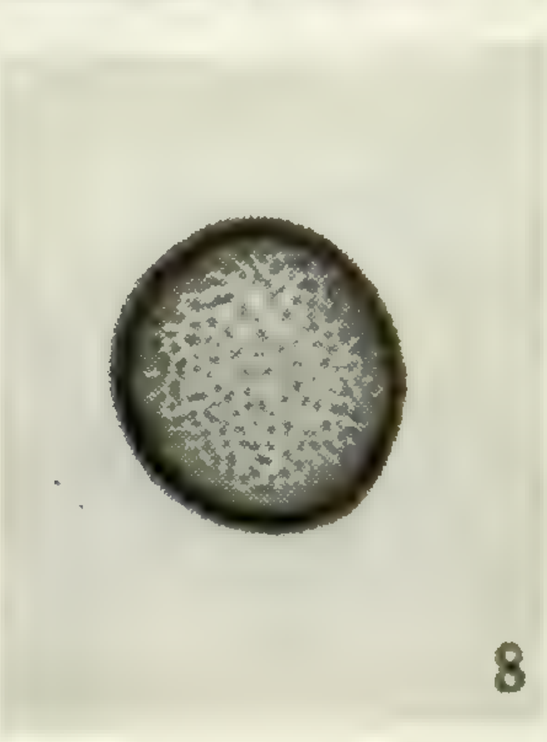
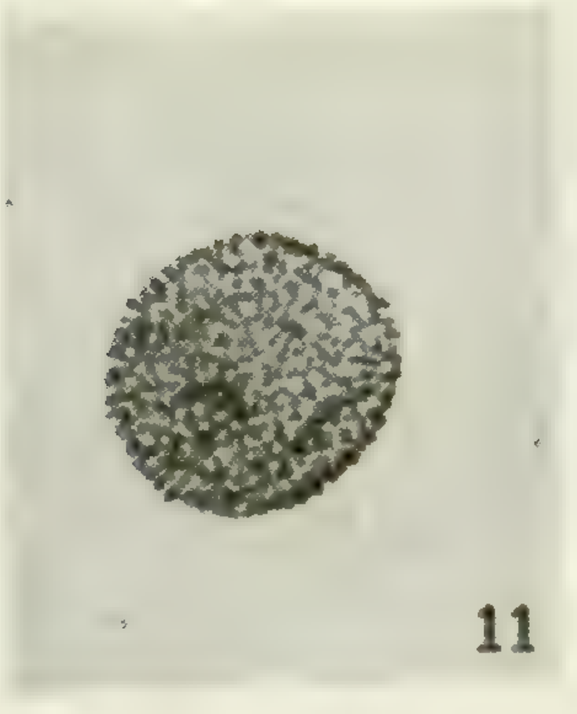


PLATE 10. FIG. 1. *Sageraea lanceolata* Miq., × 1000. FIG. 2. *Rauwenhoffia siamensis* Scheff., × 1000. FIG. 3. *Polyalthia hookeriana* King, × 200. FIG. 4–6. *P. glauca* (Hassk.) Boerl., × 1000.









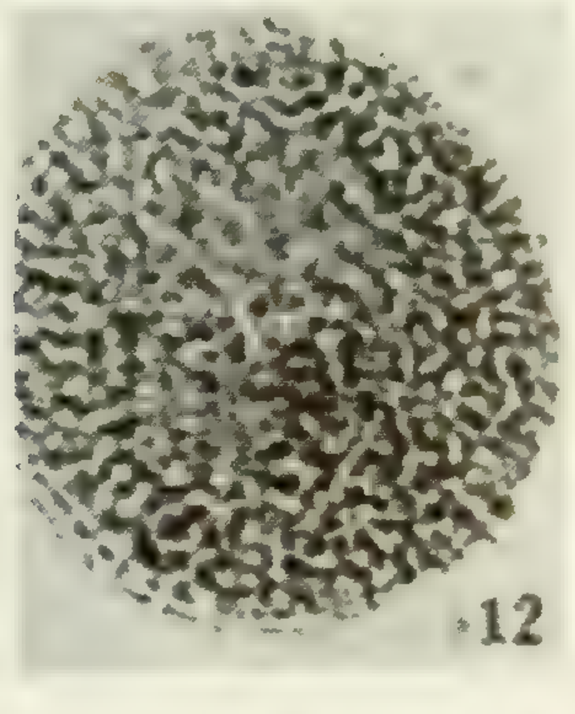
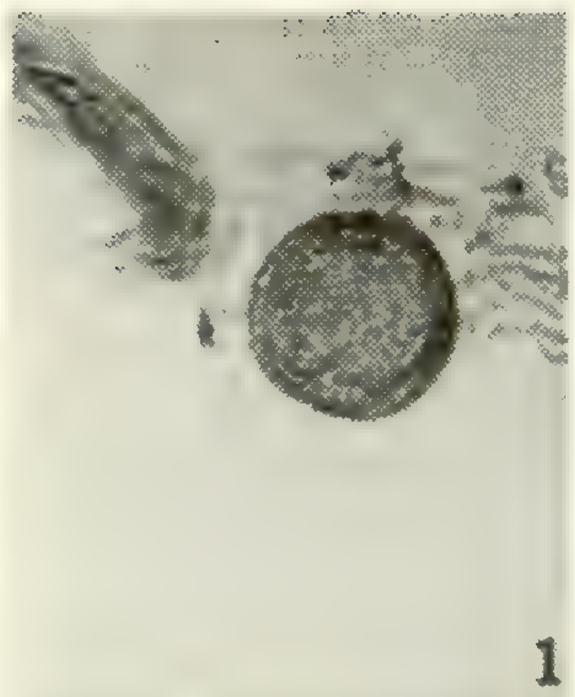


PLATE 11. FIG. 1. *Alphonsea monogyna* Merr. & Chun, × 500. FIG. 2. *Rauwenhoffia leichhardtii* (F. Muell.) Diels, × 500. FIG. 3. *Polyalthia glauca* (Hassk.) Boerl., × 500. FIG. 4,5. *P. hypoleuca* Hk.f. & Th.; Fig. 4, × 500; Fig. 5, × 1000. FIG. 6. *P. nemoralis* Aug. DC., × 500. FIG. 7. *P. laui* Merr., × 500. FIG. 8. *P. cheliensis* Hu, × 500. FIG. 9. *Chieniodendron hainanense* Tsiang & P. T. Li, × 500. FIG. 10. *Mezzettia umbellata* Becc., × 500. FIG. 11,12. *Woodiella sympetala* Merr.; Fig. 11, × 500; Fig. 12, × 1000.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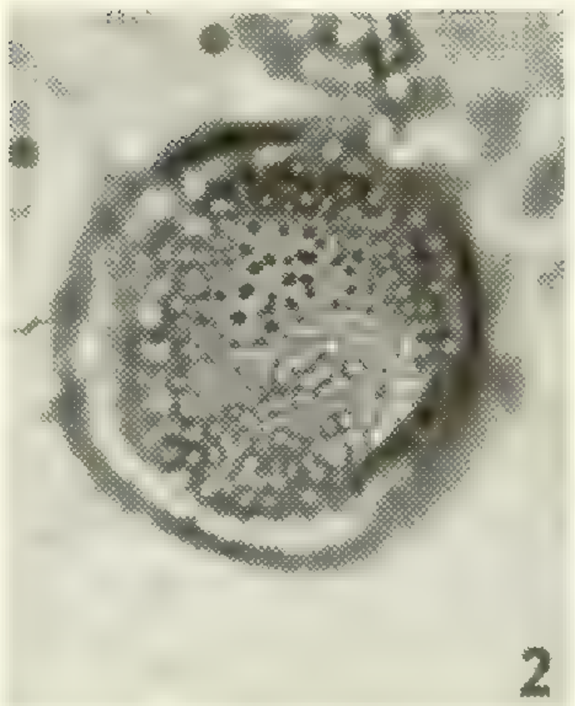
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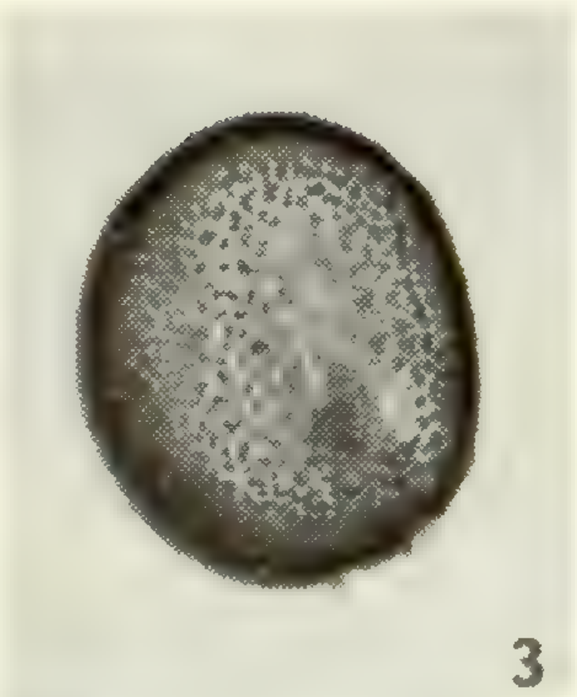
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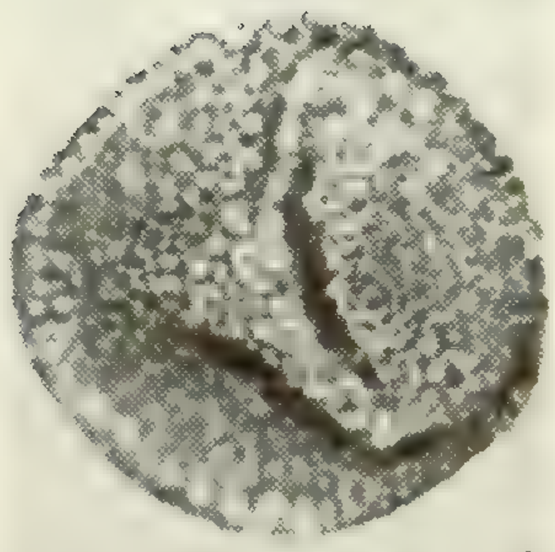
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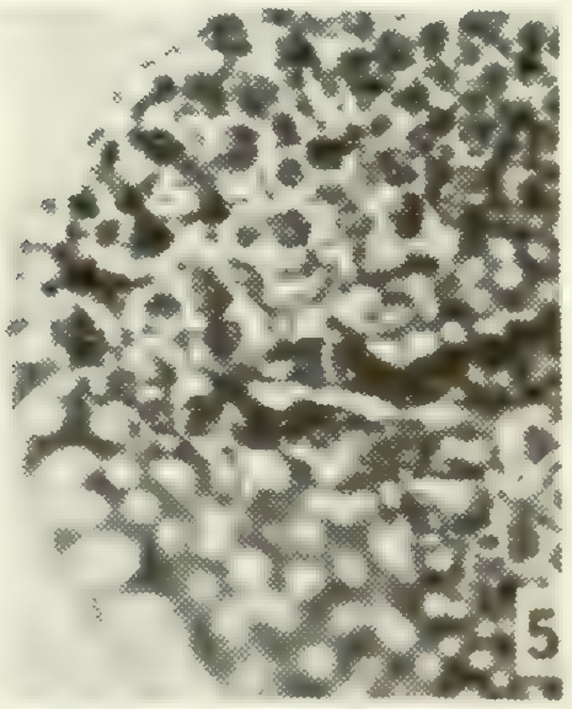
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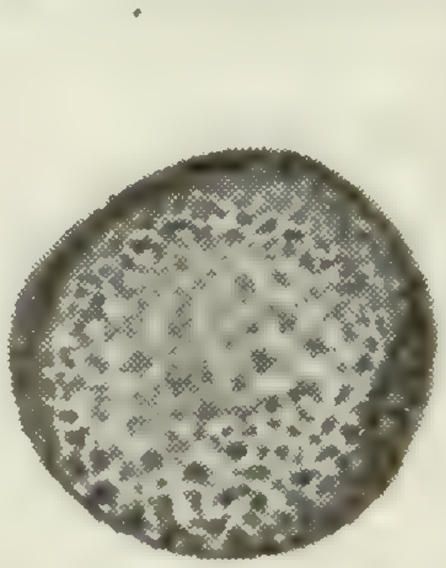
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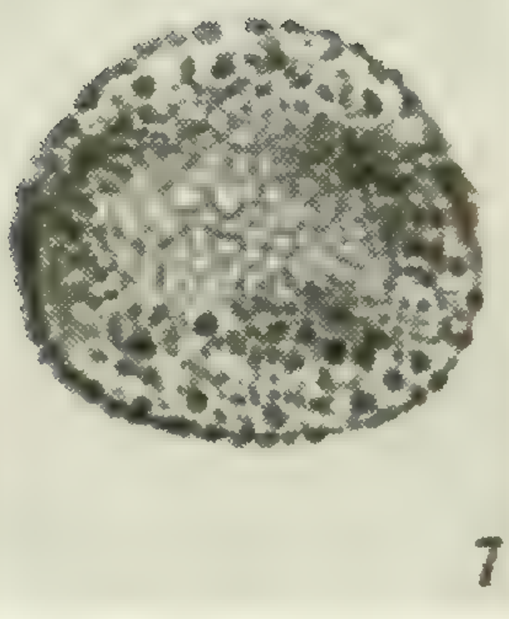
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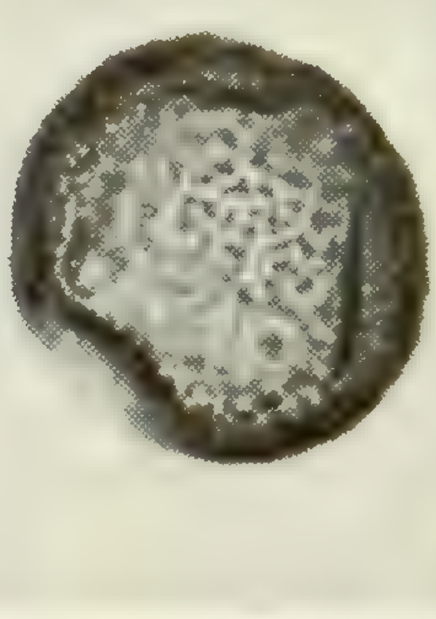
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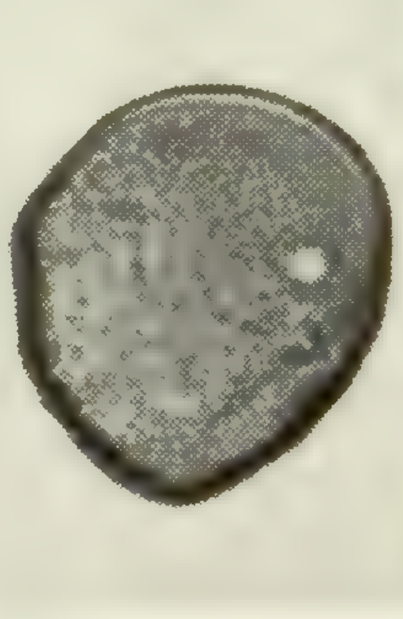
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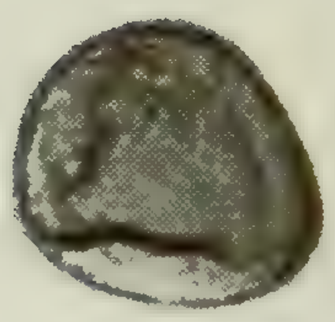
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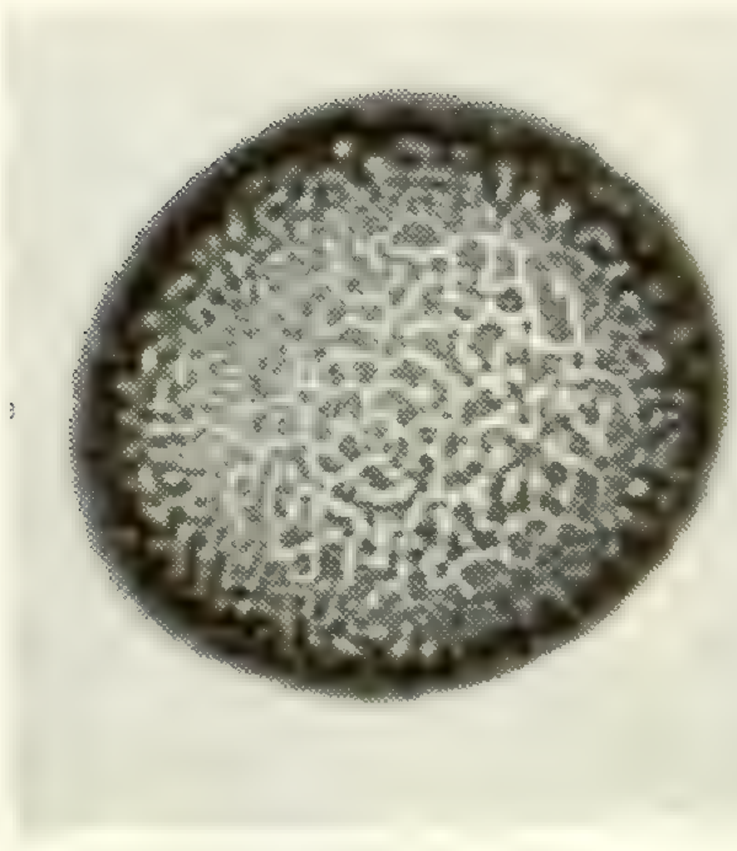
PLATE 12. FIG. 1,2. *Neouvaria acuminatissima* (Miq.) Airy-Shaw; Fig. 1, × 500; Fig. 2, × 1000. FIG. 3. *Papualthia reticulata* (Elm.) Merr., × 500. FIG. 4,5. *Miliusa chunii* W. T. Wang; Fig. 4, × 500; Fig. 5, × 1000. FIG. 6. *M. velutina* Hk.f. & Th., × 500. FIG. 7. *M. campanulata* Pierre, × 500. FIG. 8. *Saccopetalum tomentosum* Hk.f. & Th., × 500. FIG. 9. *Fissistigma acuminatissimum* Merr., × 500. FIG. 10. *Mitrella kentii* (Bl.) Miq., × 500. FIG. 11. *Melodorum aberrans* (Maingay ex Hk.f. & Th.) J. Sincl., × 500. FIG. 12. *Oncodostigma monosperma* (Hk.f. & Th.) J. Sincl., × 500.



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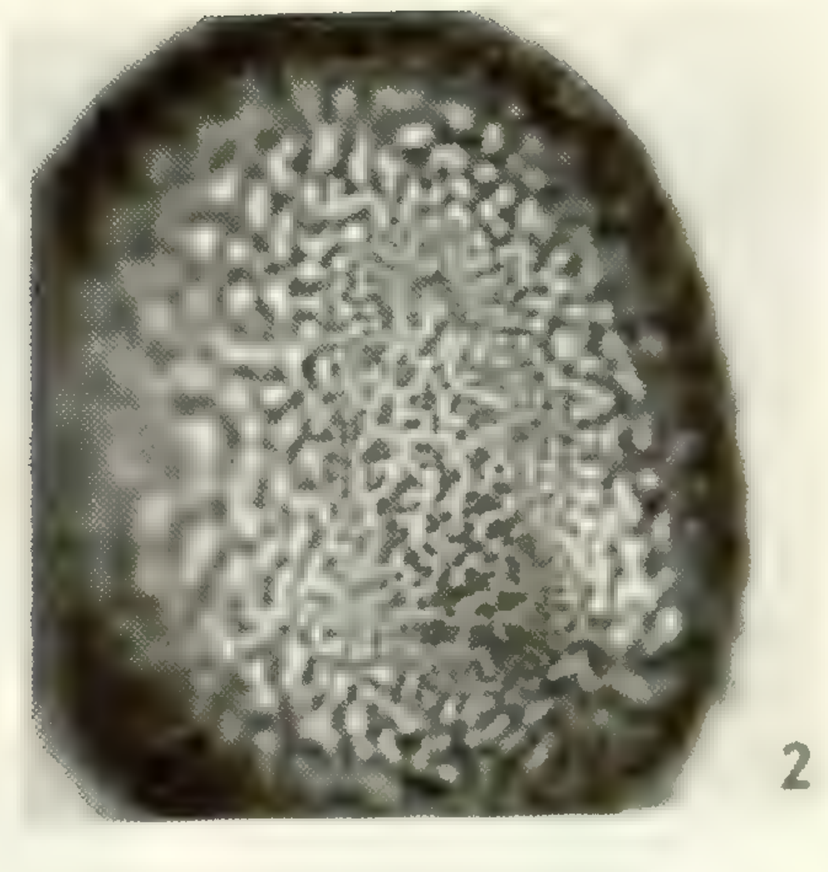

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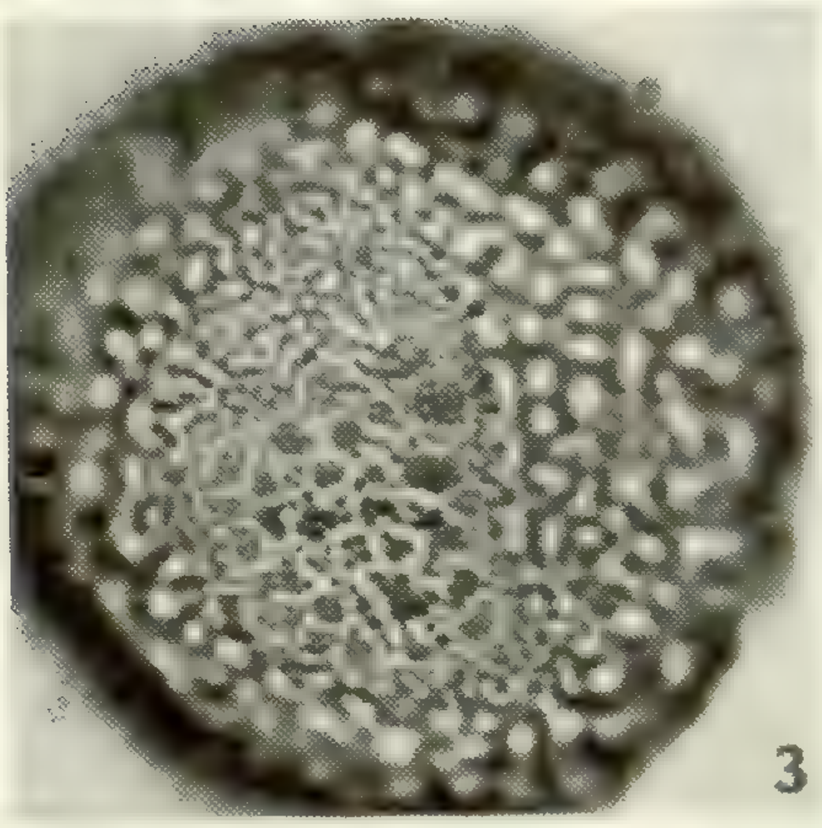

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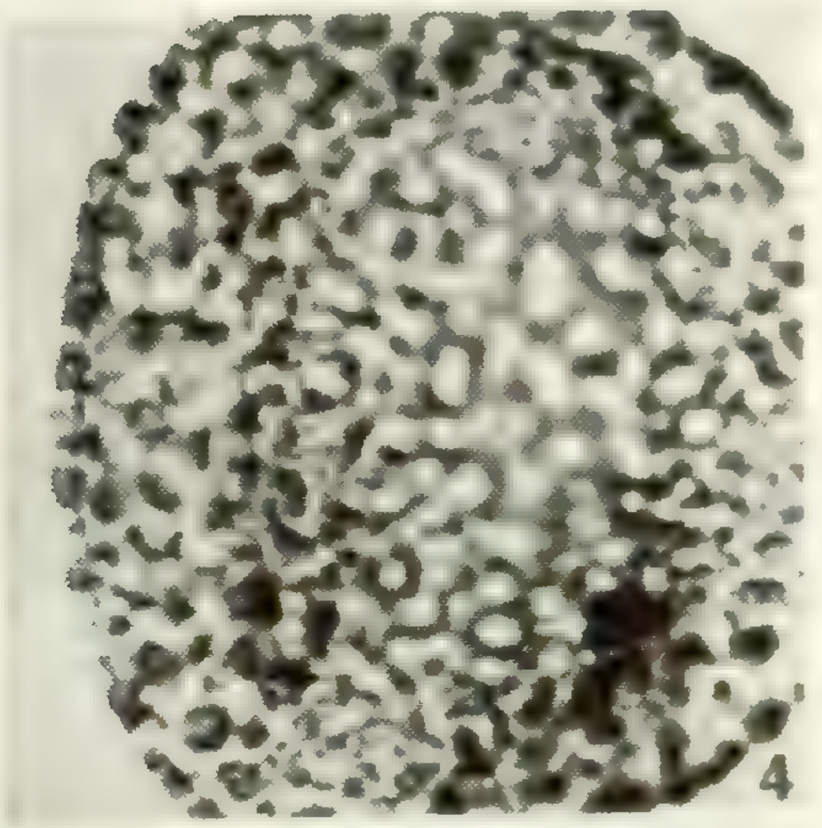

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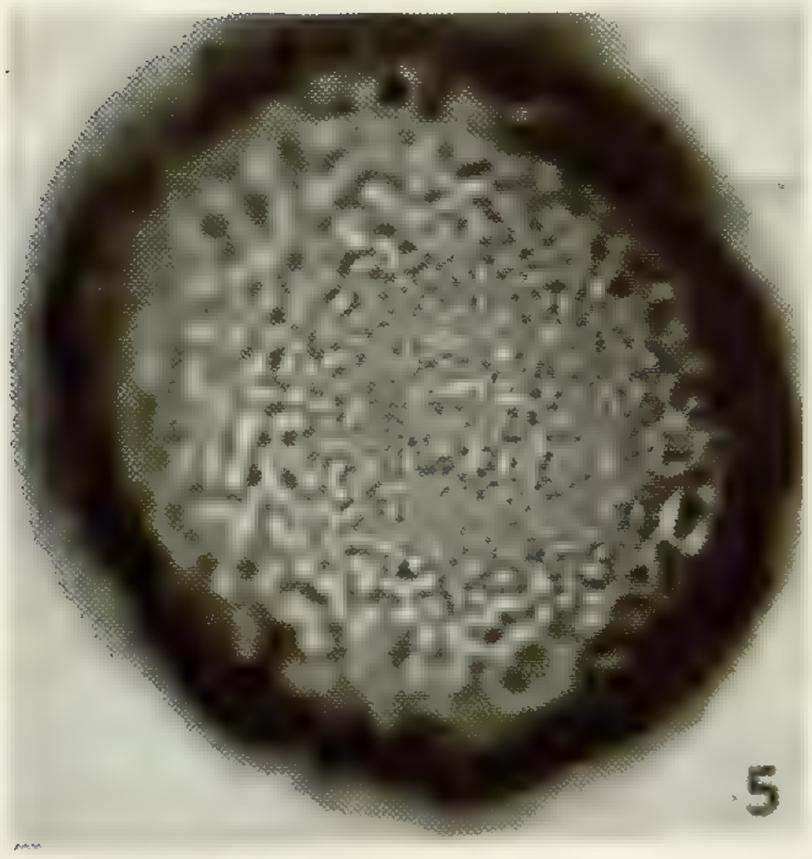

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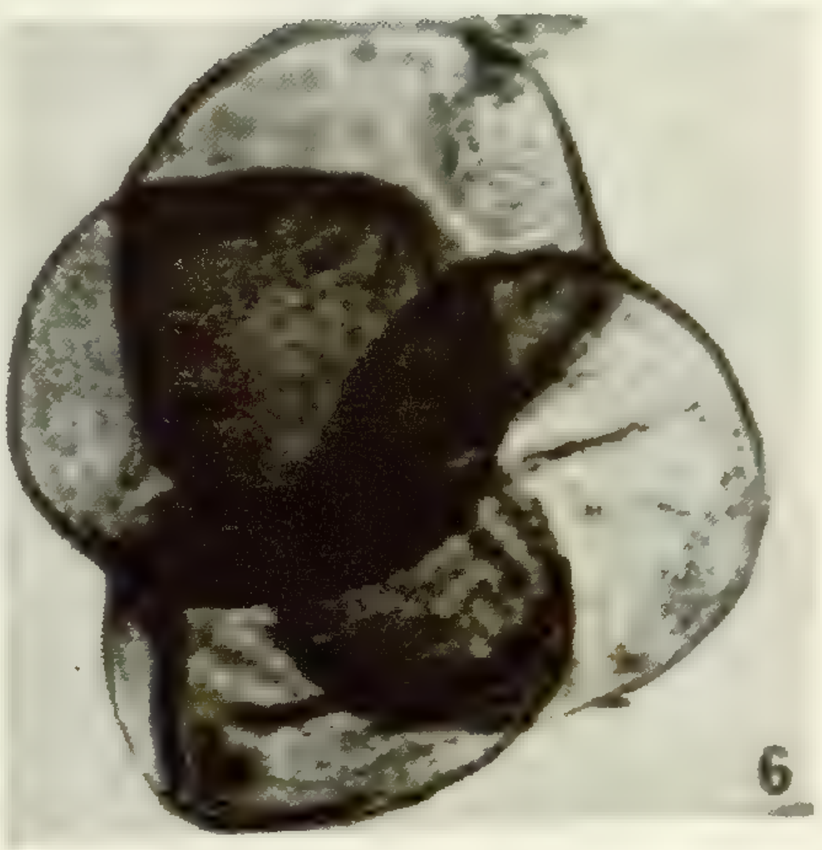
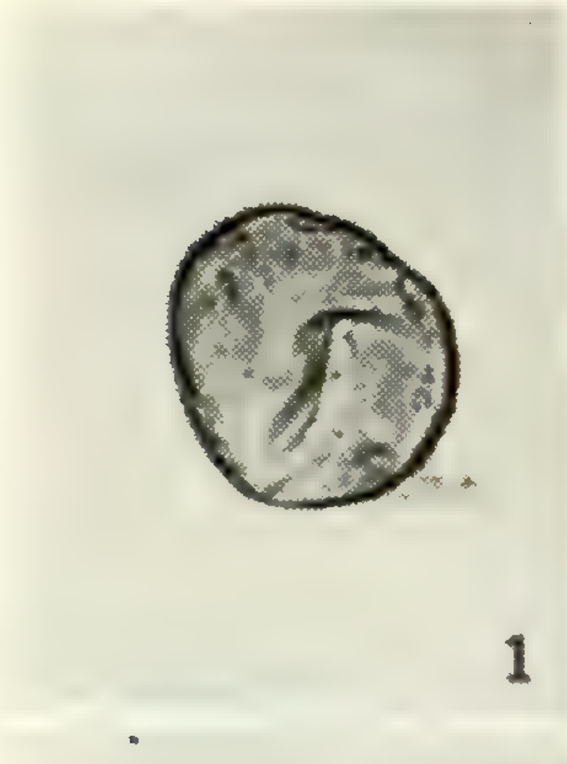


6

PLATE 13. FIG. 1. *Polyalthia cheliensis* Hu, × 1000. FIG. 2. *Papualthia reticulata* (Elm.) Merr., × 1000. FIG. 3. *Miliusa velutina* Hk.f. & Th., × 1000. FIG. 4. *M. campanulata* Pierre, × 1000. FIG. 5. *Artabotrys uncinatus* (Lam.) Merr., × 1000. FIG. 6. *Mitrephora macrantha* Hassk., × 500.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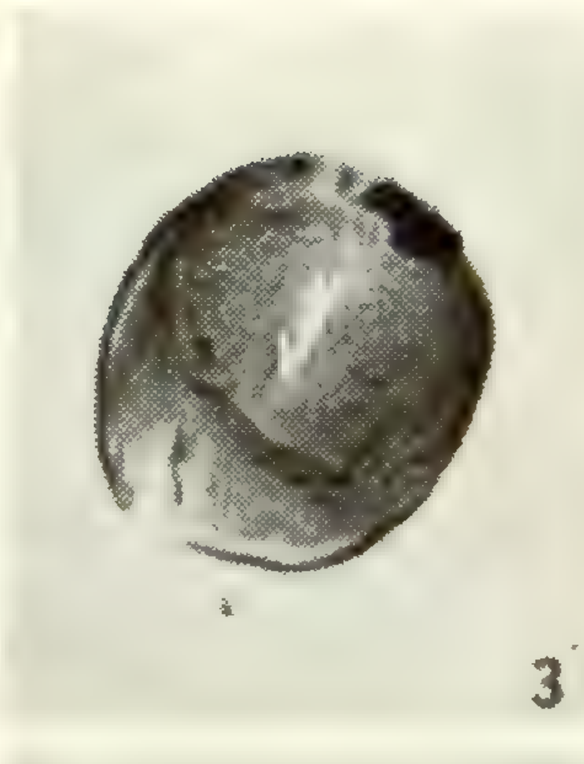
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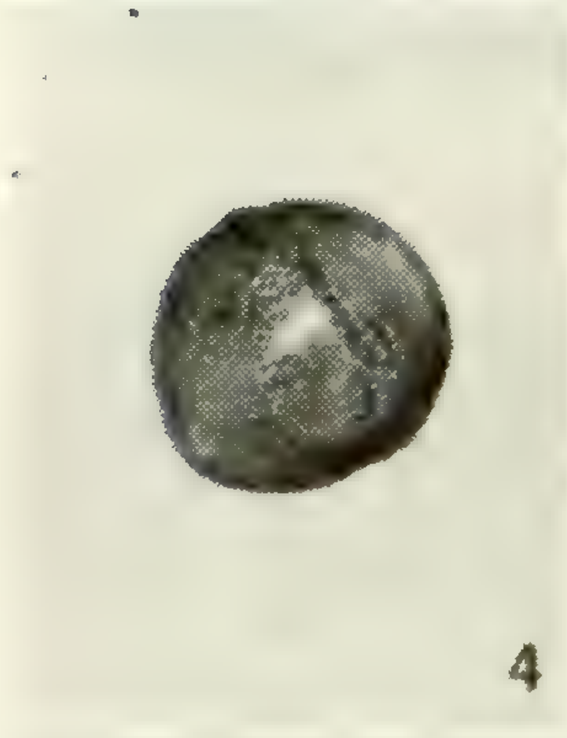
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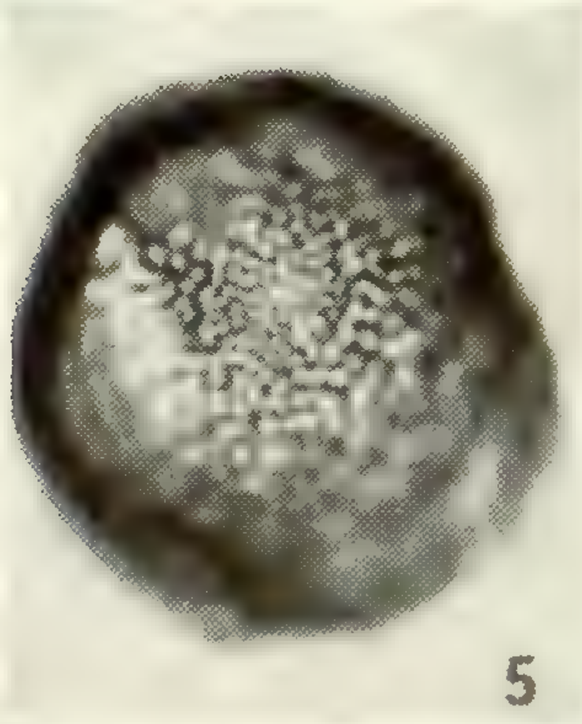
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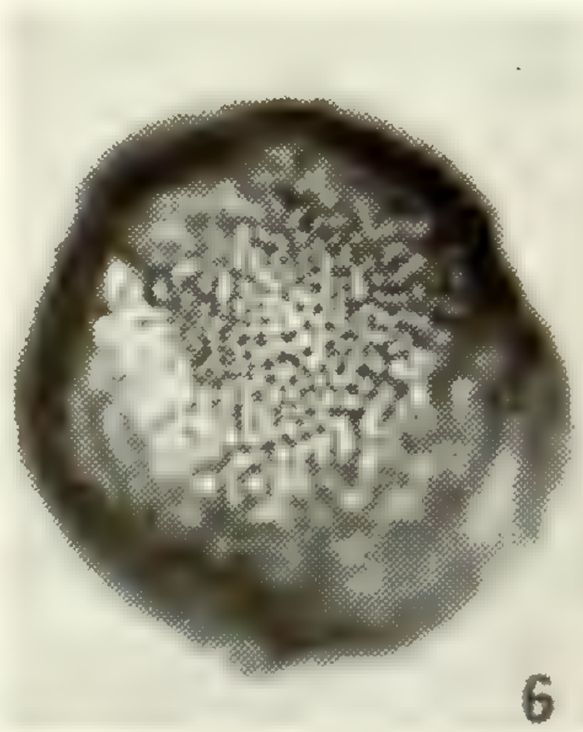
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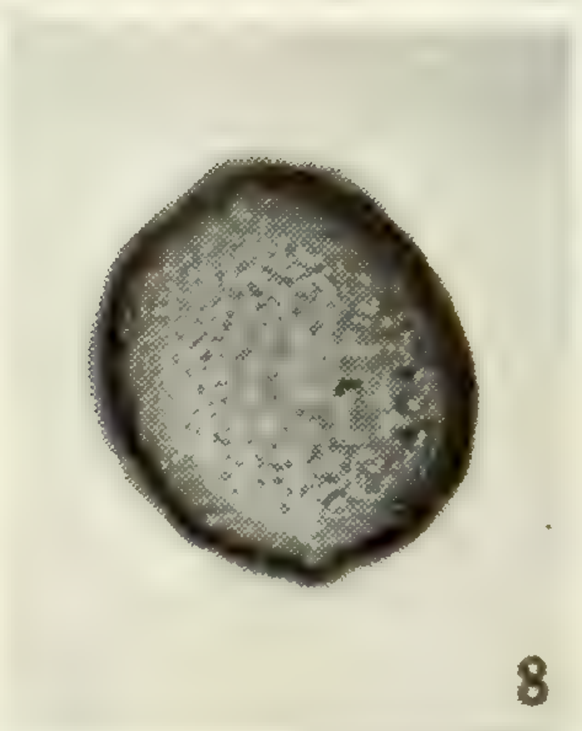
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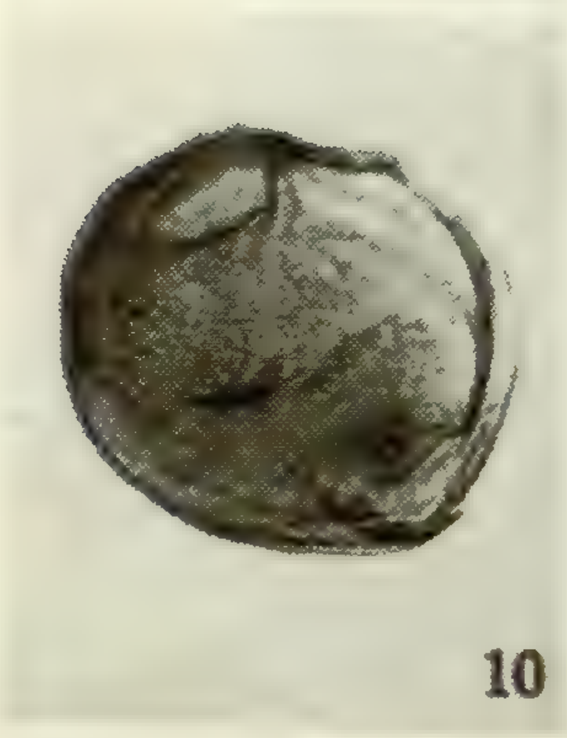
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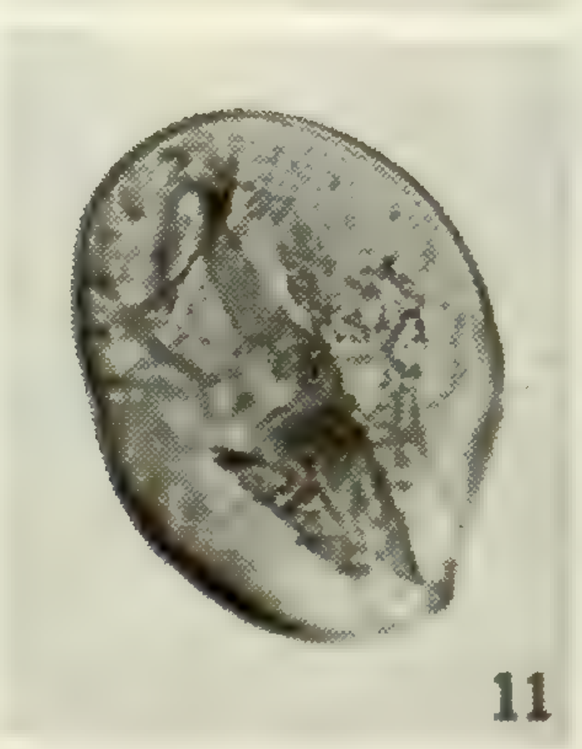
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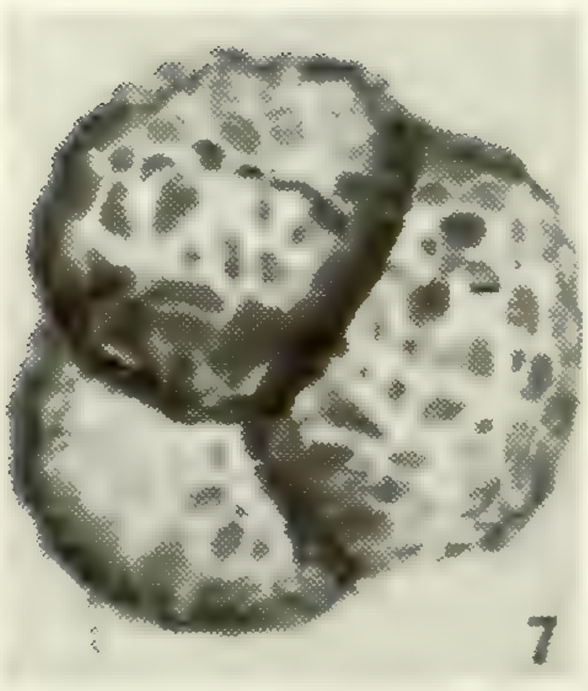
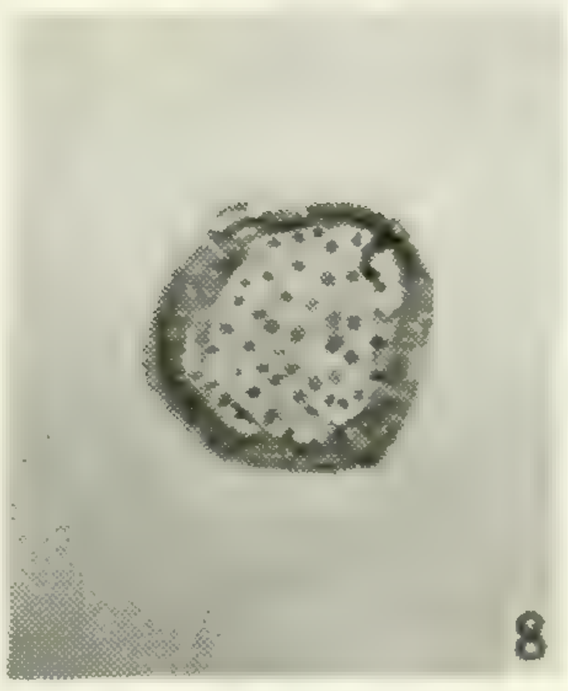
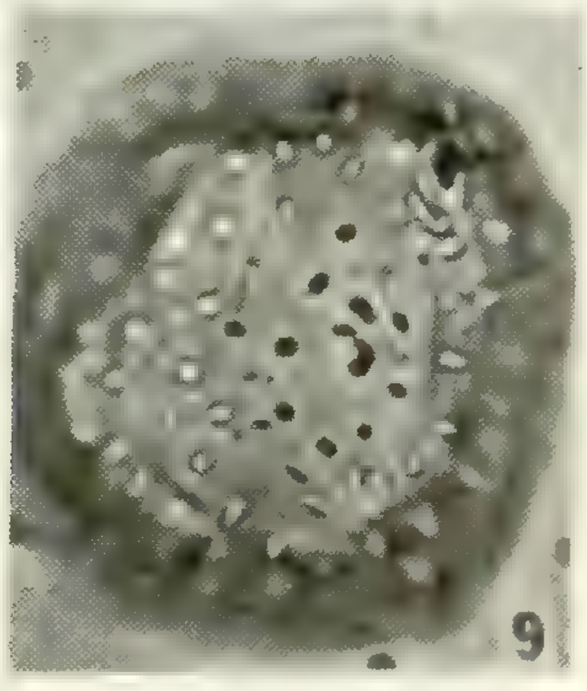
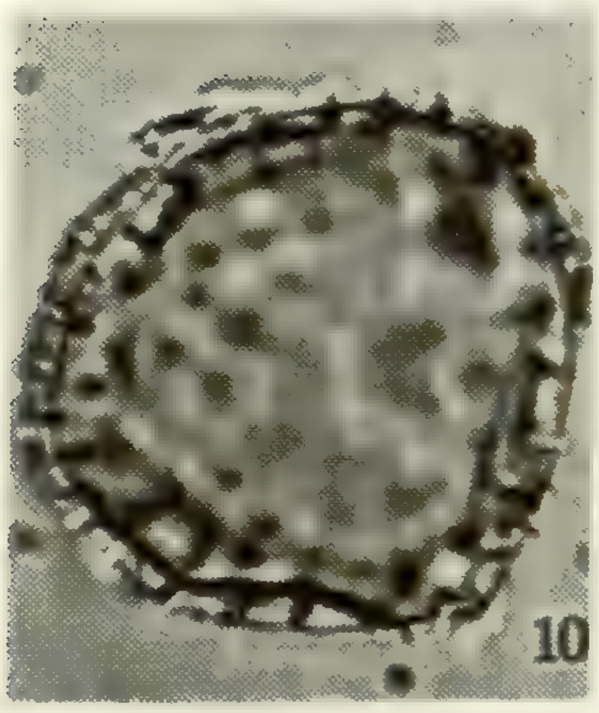
PLATE 14. FIG. 1,2. *Guamia mariannae* (Saff.) Merr.; Fig. 1, × 500; Fig. 2, × 1000. FIG. 3. *Artabotrys trichopetalus* Merr., × 500. FIG. 4–6. *A. suaveolens* (Bl.) Bl.; Fig. 4, × 500; Fig. 5,6, × 1000. FIG. 7. *A. stenopetalus* Engl., × 500. FIG. 8. *A. uncinatus* (Lam.) Merr., × 500. FIG. 9. *Cyathocalyx papuanus* Diels, × 500. FIG. 10. *C. insularis* A. C. Smith, × 500. FIG. 11. *Drepananthus philippinensis* Merr., × 500. FIG. 12. *Orophea leytensis* Merr., × 500.









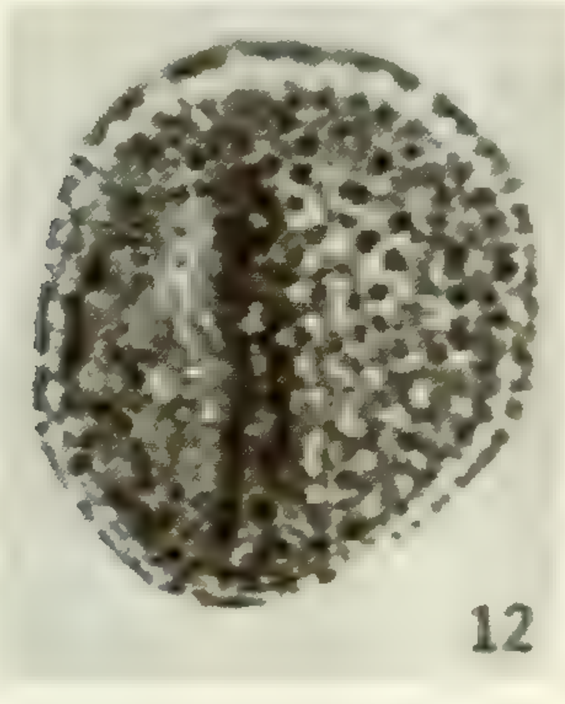


PLATE 15. FIG. 1. *Orophea vulcanica* Elm., × 500. FIG. 2. *Platymitra macrocarpa* Boerl., × 500. FIG. 3. *Pseuduvaria philippinensis* Merr., × 500. FIG. 4. *P. versteegii* (Diels) Merr., × 500. FIG. 5. *P. reticulata* (Bl.) Miq., × 500. FIG. 6. *P. rugosa* (Bl.) Merr., × 500. FIG. 7. *Orophea luzonensis* Merr., × 500. FIG. 8–10. *Popowia heterantha* (H. Baill.) Diels; Fig. 8, × 500; Fig. 9,10, × 1000. FIG. 11,12. *P. gracilis* Oliv. ex Engl. & Diels; Fig. 11, × 500; Fig. 12, × 1000.

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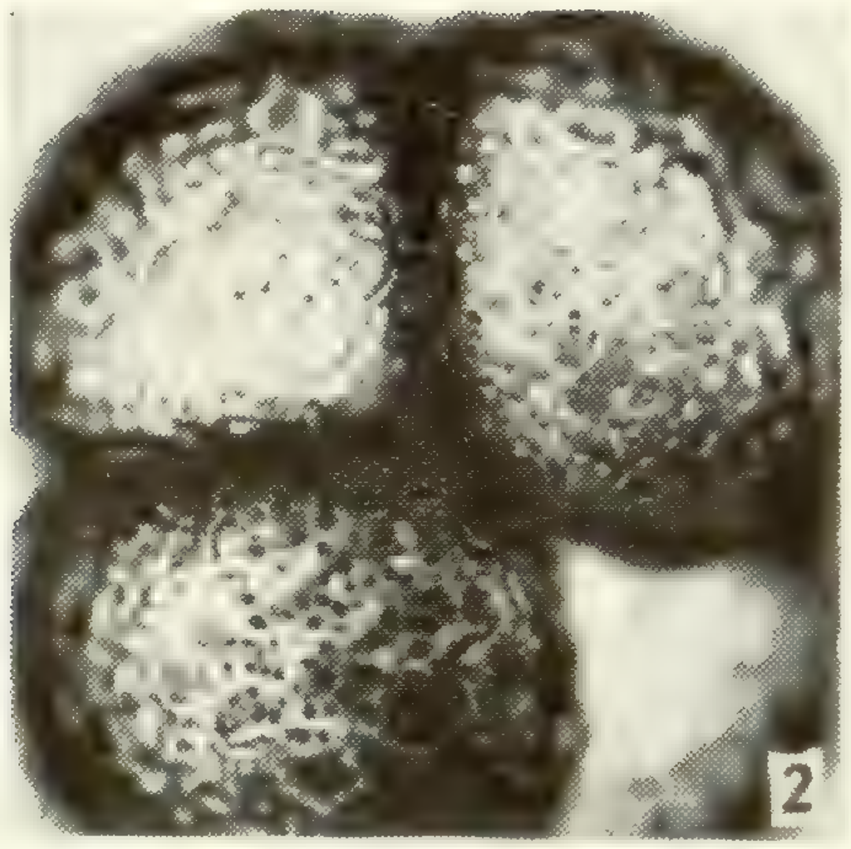
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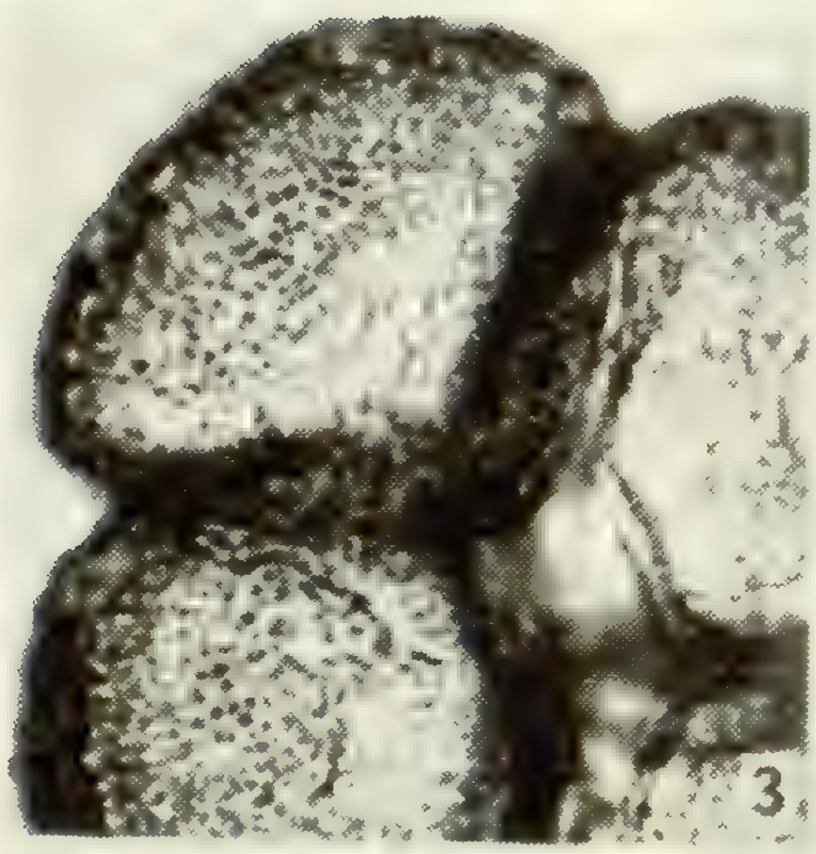
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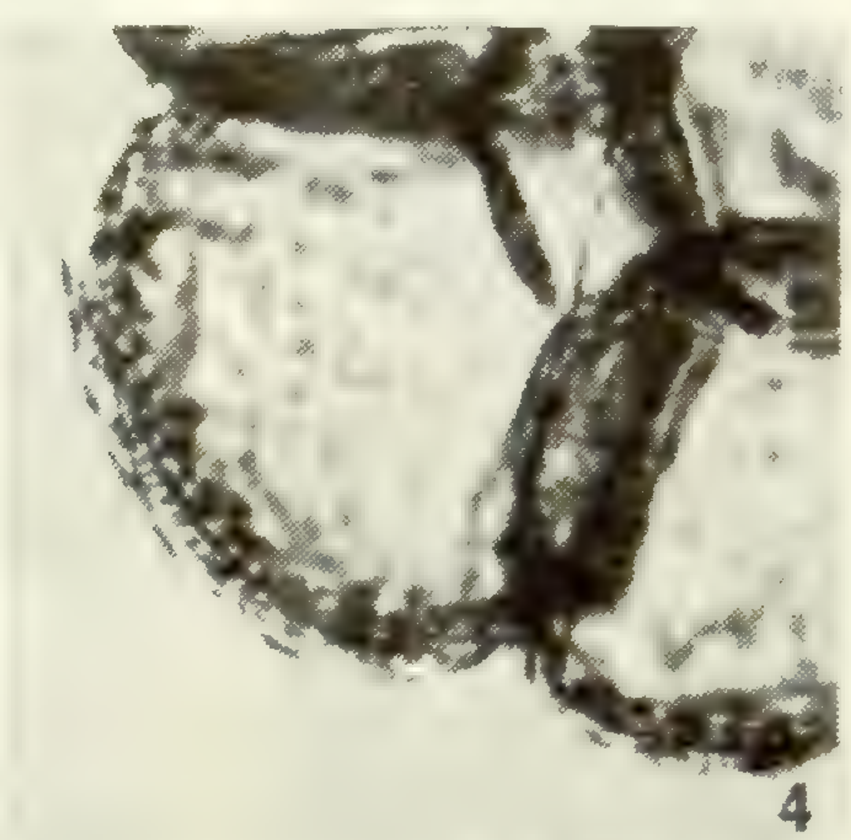
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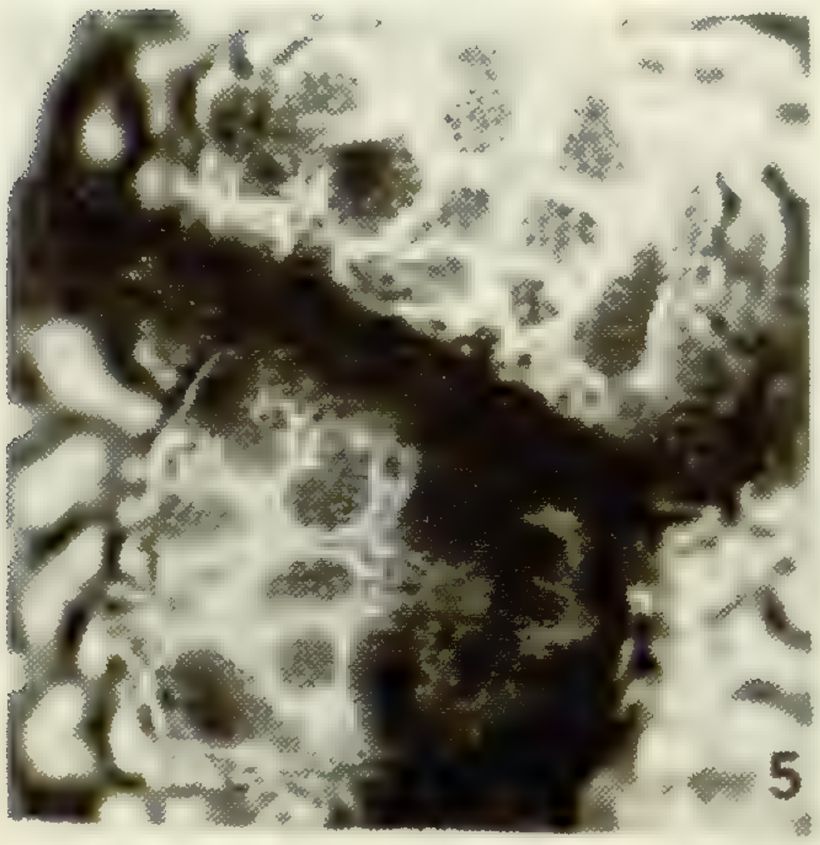
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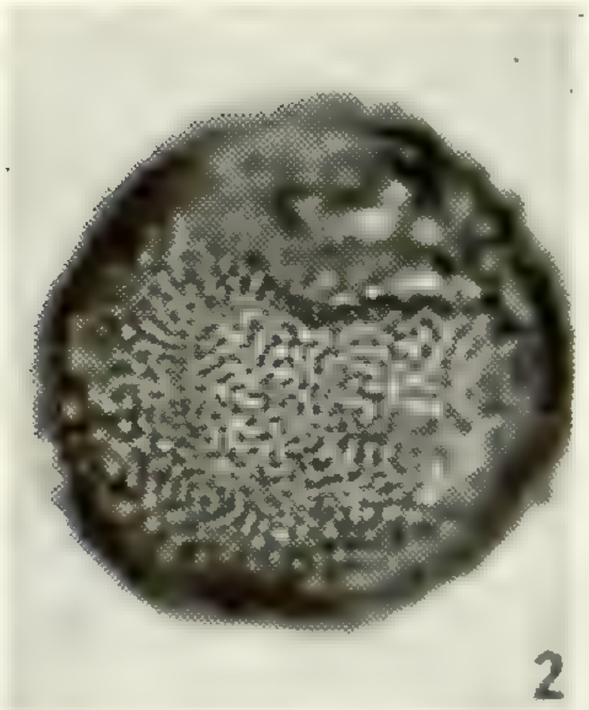
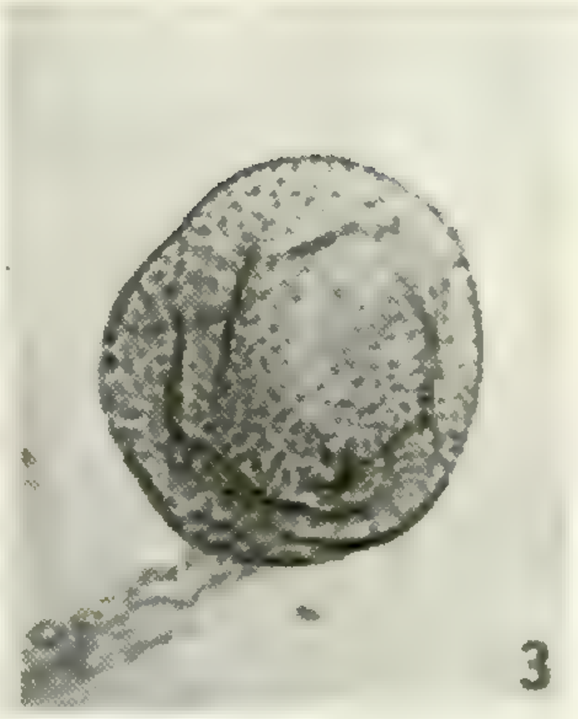
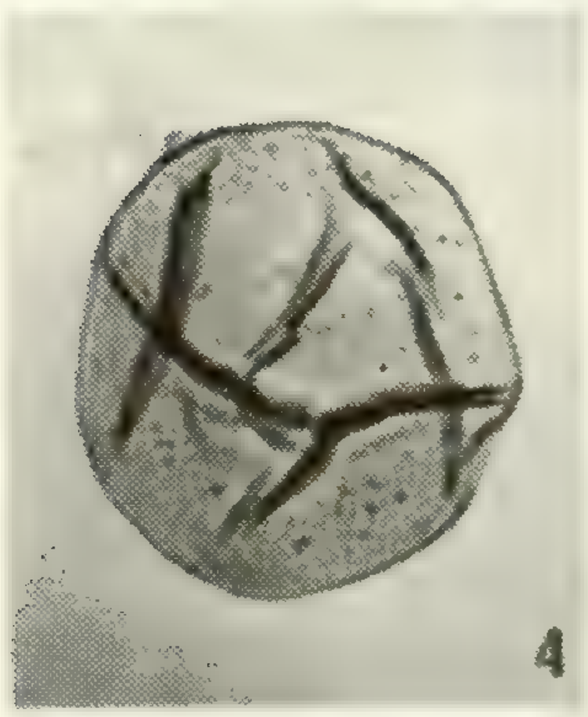
PLATE 16. FIG. 1. *Mitrephora williamsii* C. B. Rob., × 500. FIG. 2. *Pseuduvaria reticulata* (Bl.) Miq., × 1000. FIG. 3,4. *P. rugosa* (Bl.) Merr., × 1000. FIG. 5. *Orophea luzonensis* Merr., × 1000. FIG. 6. *Phaeanthus crassipetalus* Becc., × 1000.







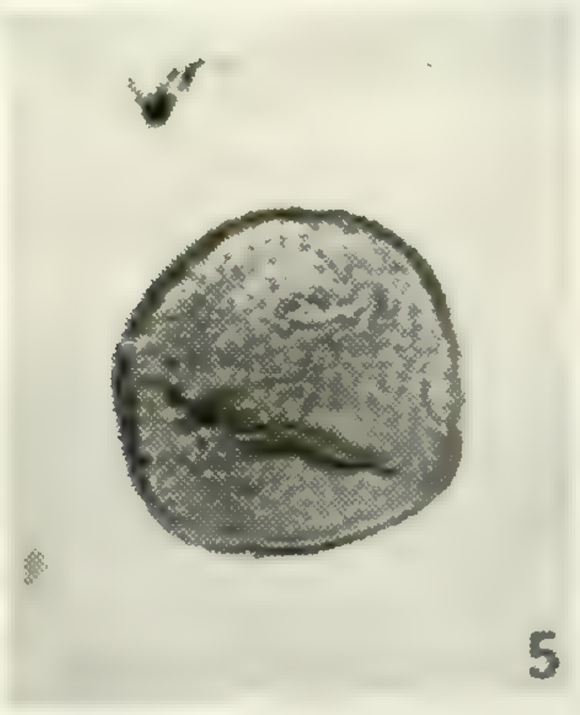
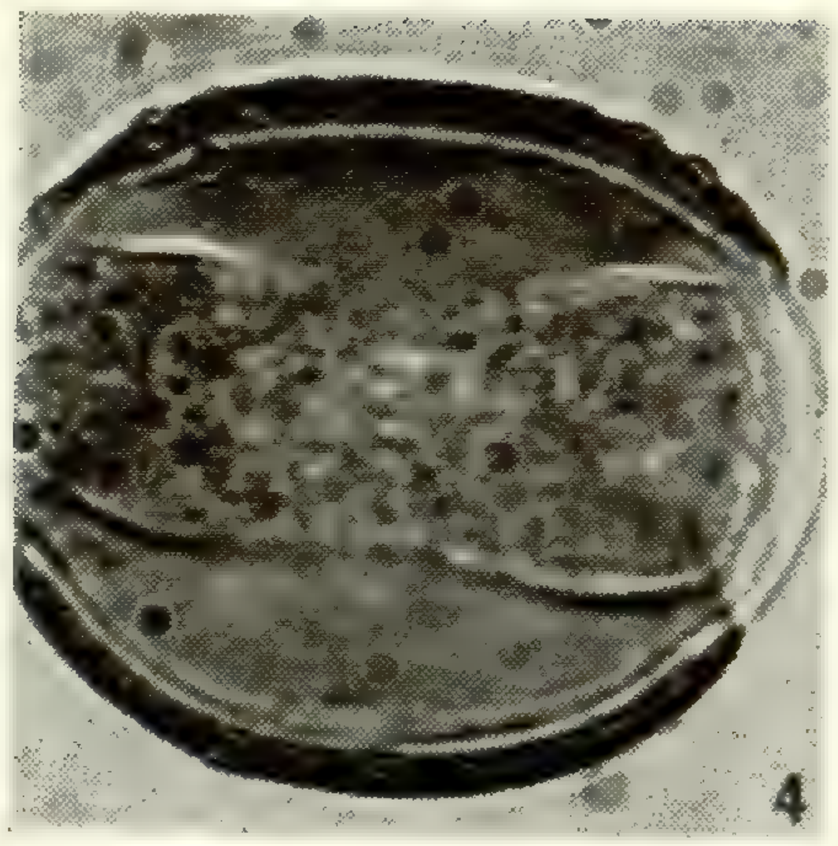
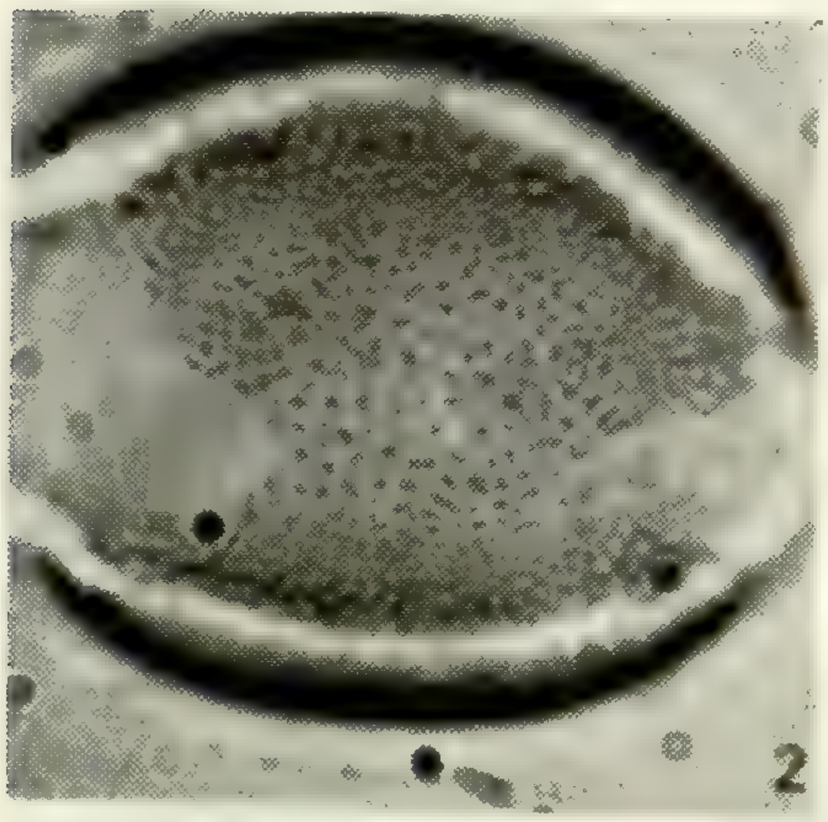
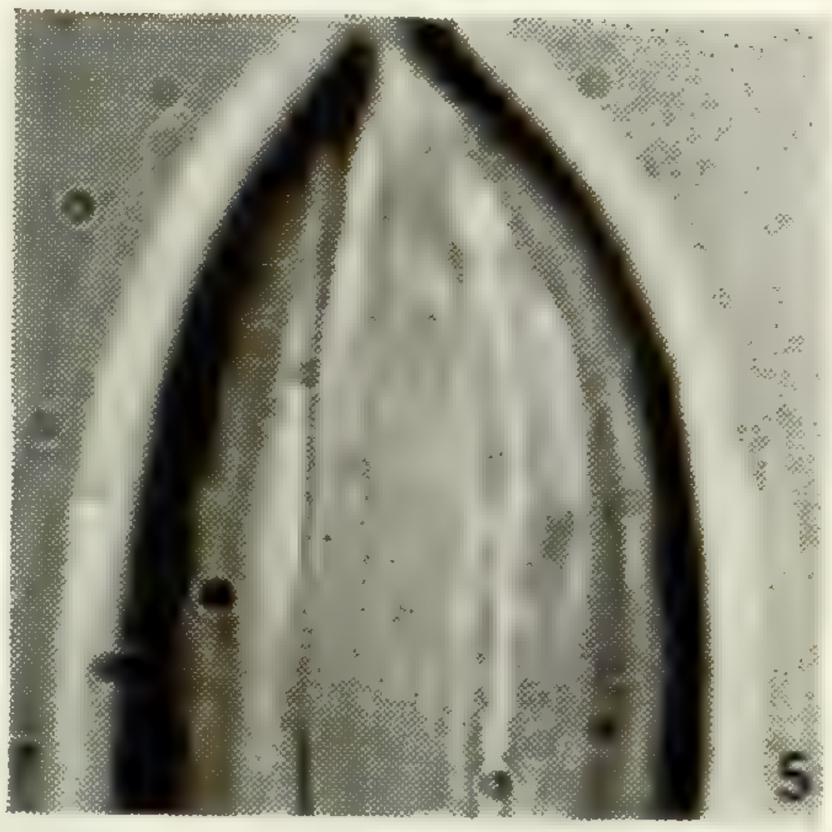
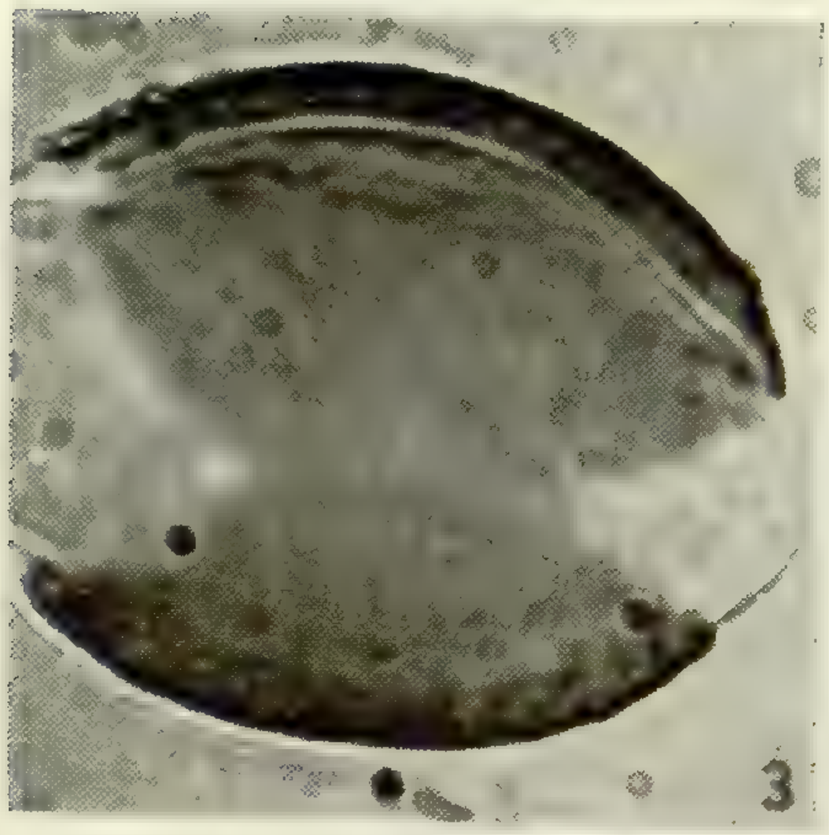


PLATE 17. FIG. 1,2. *Popowia pisocarpa* (Bl.) Endl.; Fig. 1, × 500; Fig. 2, × 1000. FIG. 3. *Phaeanthus crassipetalus* Becc., × 500. FIG. 4. *P. ebracteolatus* (Presl.) Merr., × 500. FIG. 5. *Trivalvaria macrophylla* (Bl.) Miq., × 500. FIG. 6. *Sapranthus palanga* R. E. Fries, × 500. FIG. 7. *S.* sp., × 500. FIG. 8. *Guatteria oliviformis* Donn. Smith, × 500. FIG. 9. *Guatteriopsis sessiliflora* (Benth.) R. E. Fries, × 500. FIG. 10–12. *Heteropetalum brasiliense* Benth., × 500.









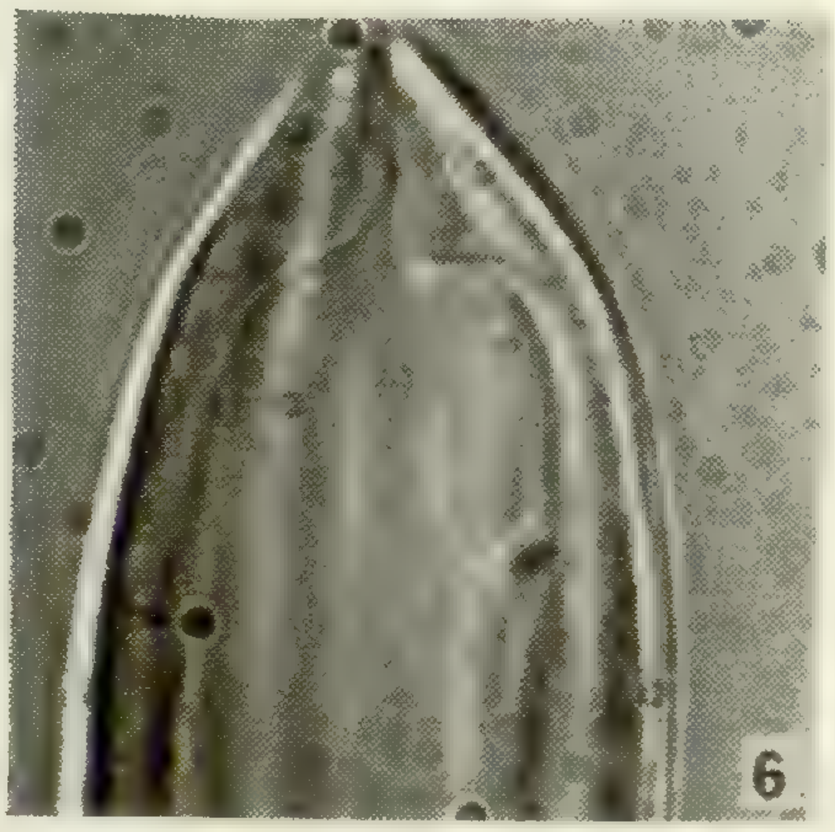
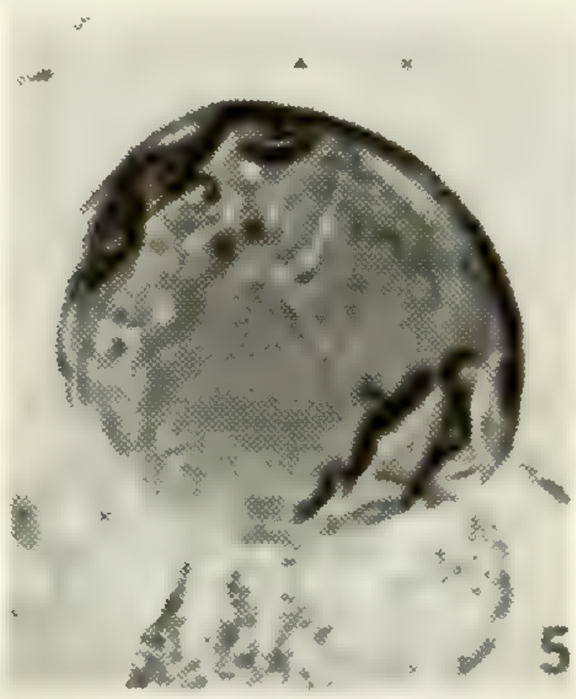
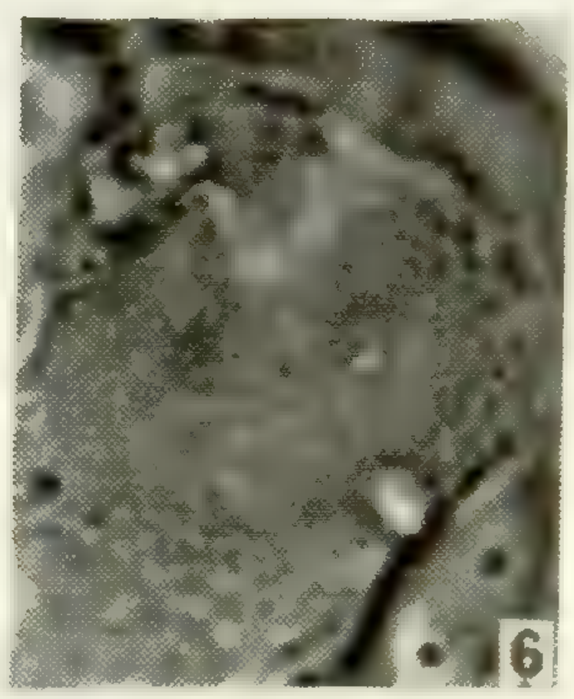
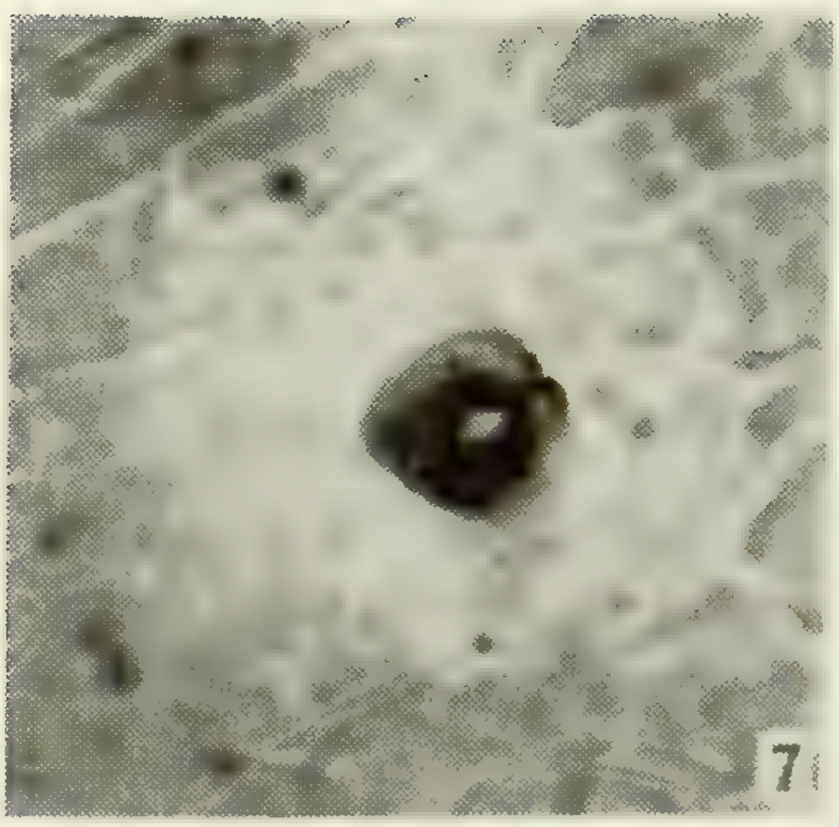


PLATE 18. FIG. 1. *Sapranthus palanga* R. E. Fries, × 1000. FIG. 2–4. *S.* sp., × 1000. FIG. 5,6. *Guatteria oliviformis* Donn. Smith, × 1000.







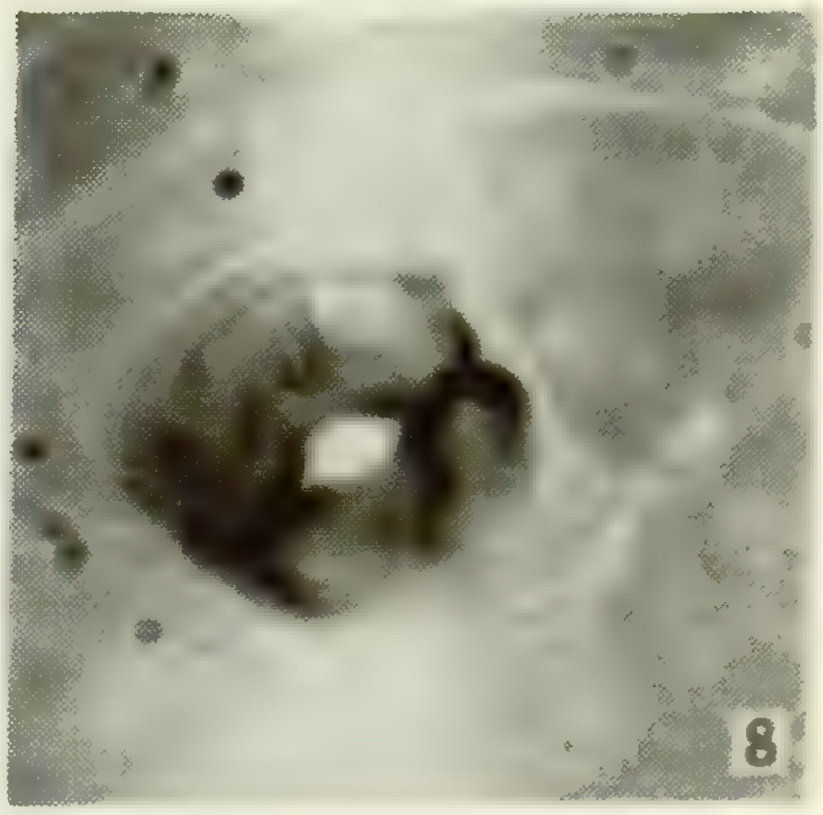
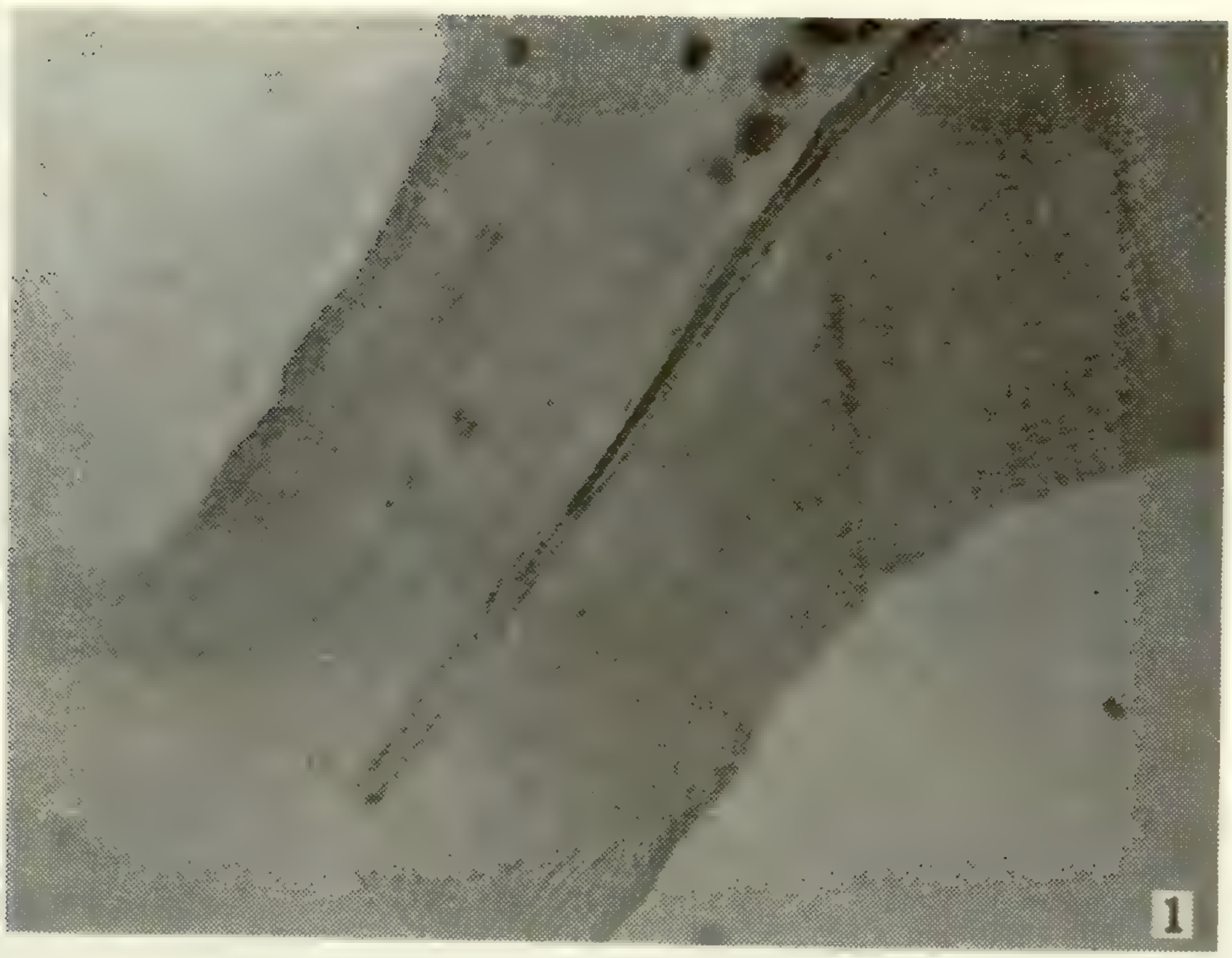


PLATE 19. FIG. 1. *Anaxagorea brevipes* Benth. in Hk.f., × 500. FIG. 2,3. *A. dolichocarpa* Sprague & Sandw., × 500. FIG. 4. *A. acuminata* (Dun.) St. Hil. ex A. DC., × 500. FIG. 5–8. *A. costaricensis* R. E. Fries; Fig. 5,7, × 500; Fig. 6,8, × 1000.



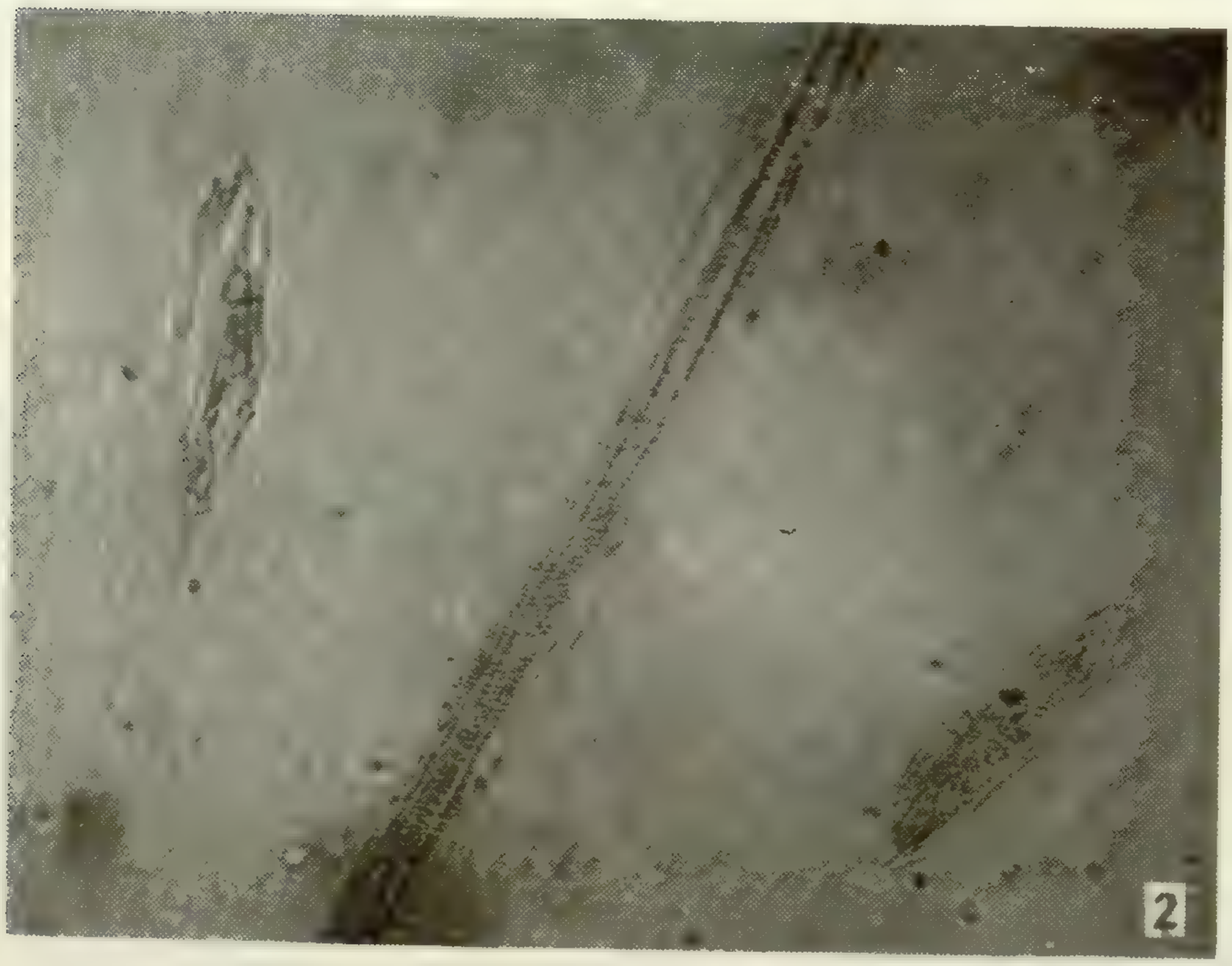
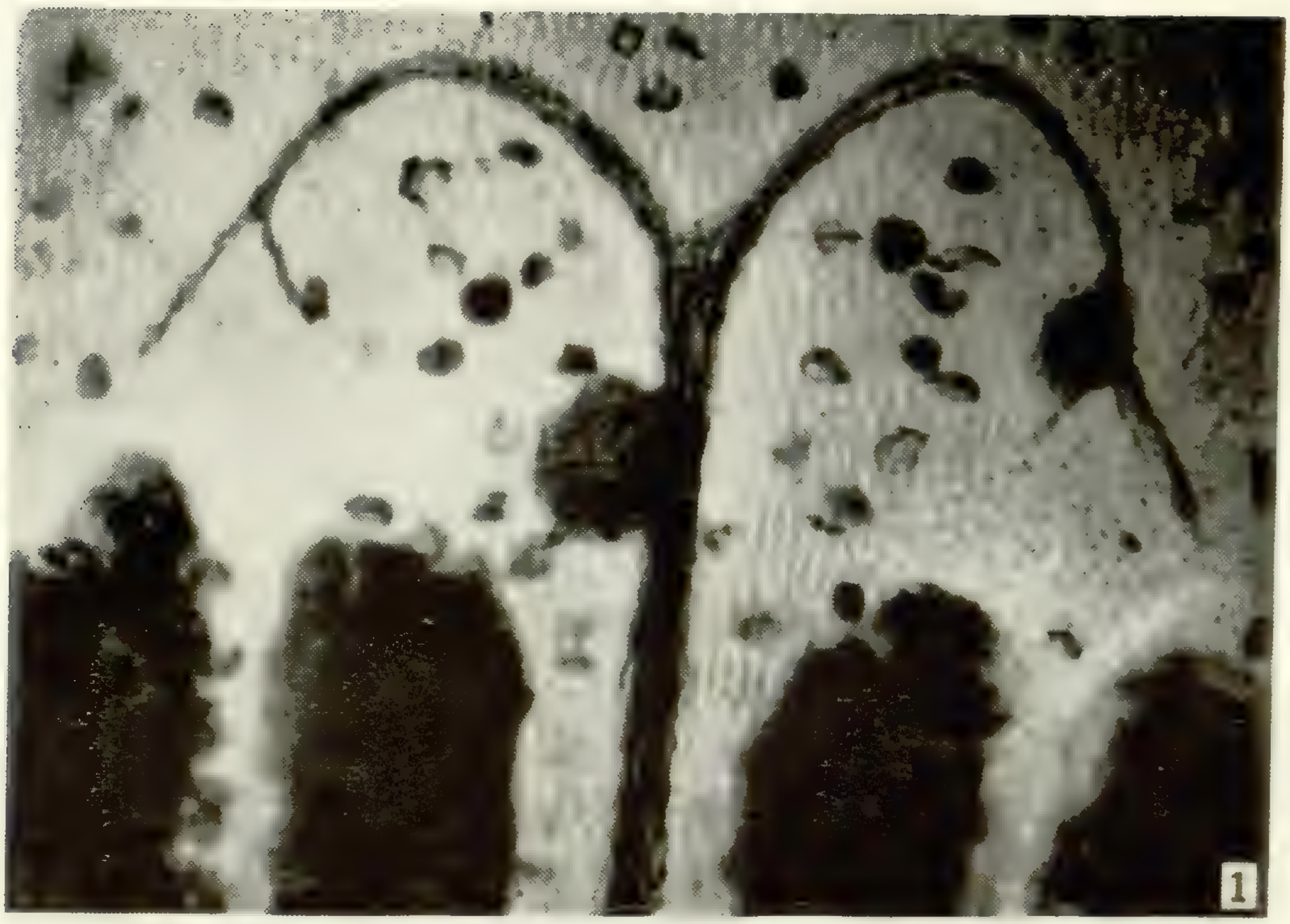


PLATE 20. FIG. 1,2. *Anaxagorea costaricensis* R. E. Fries; Fig. 1, × 100; Fig. 2, × 200.



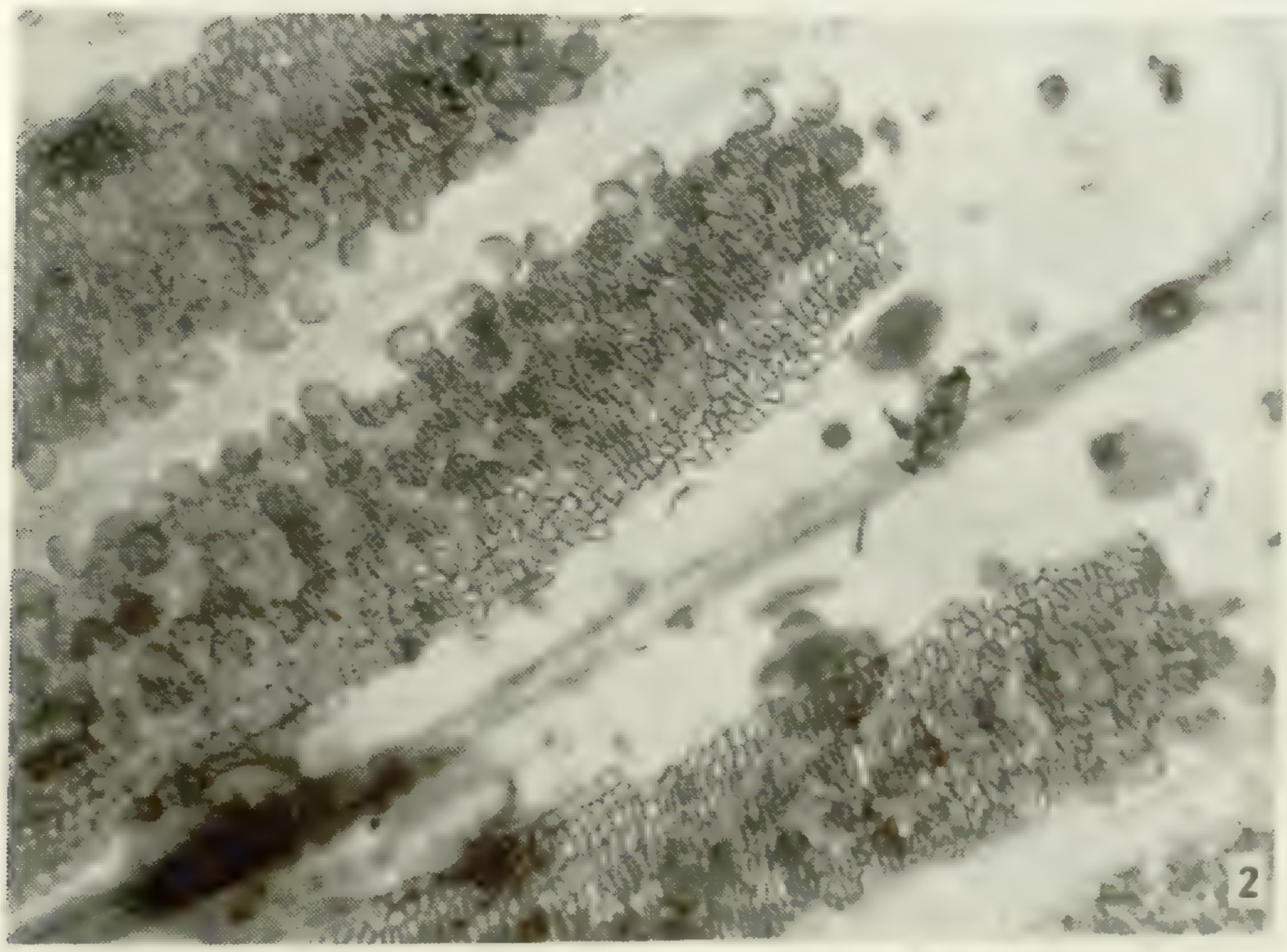
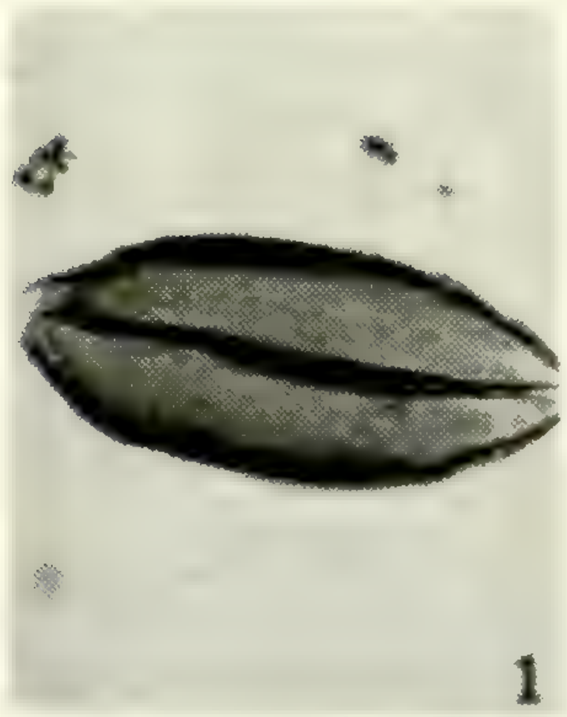


PLATE 21. FIG. 1,2. *Anaxagorea costaricensis* R. E. Fries, × 100.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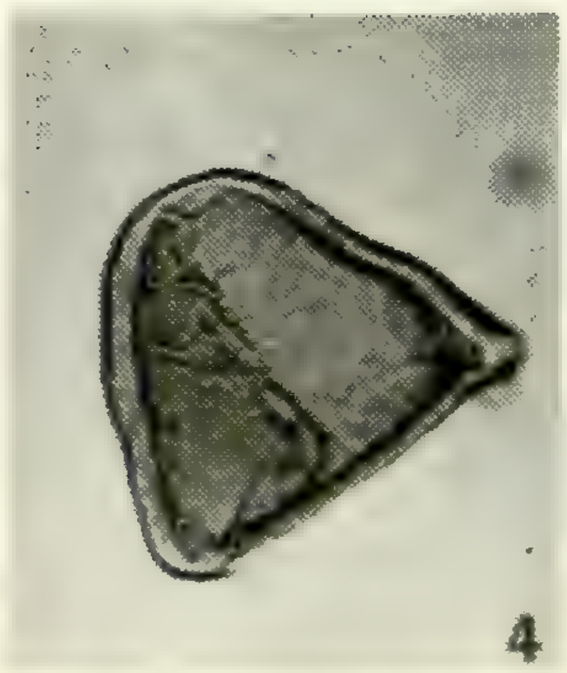
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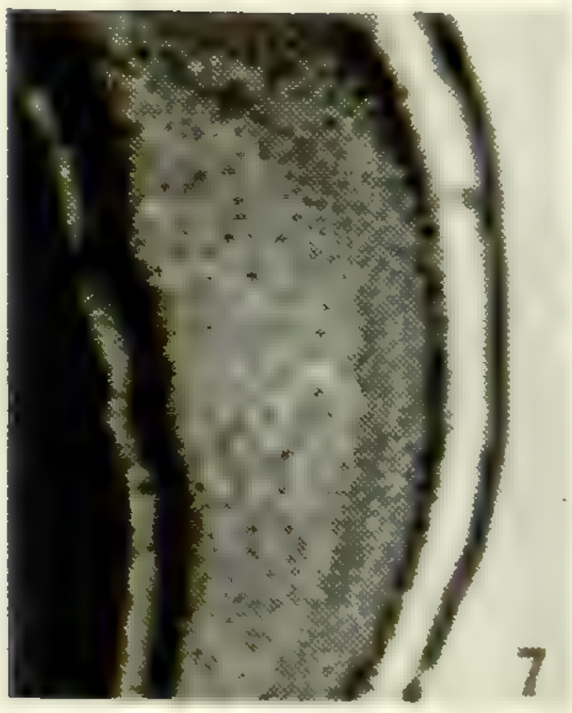
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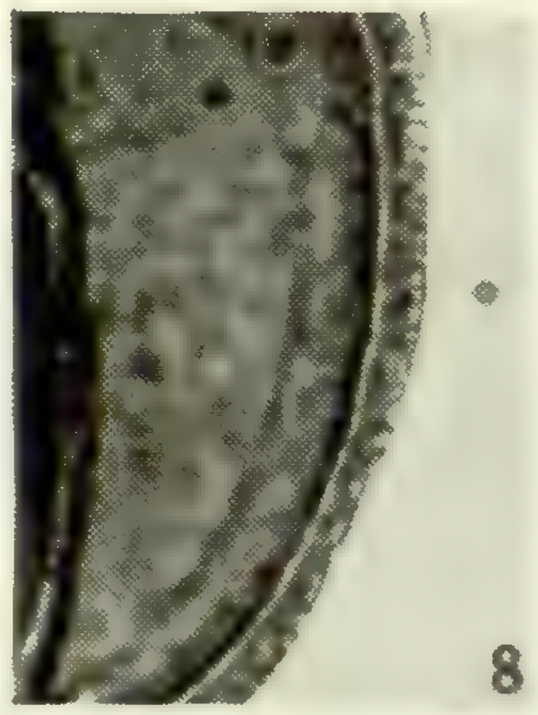
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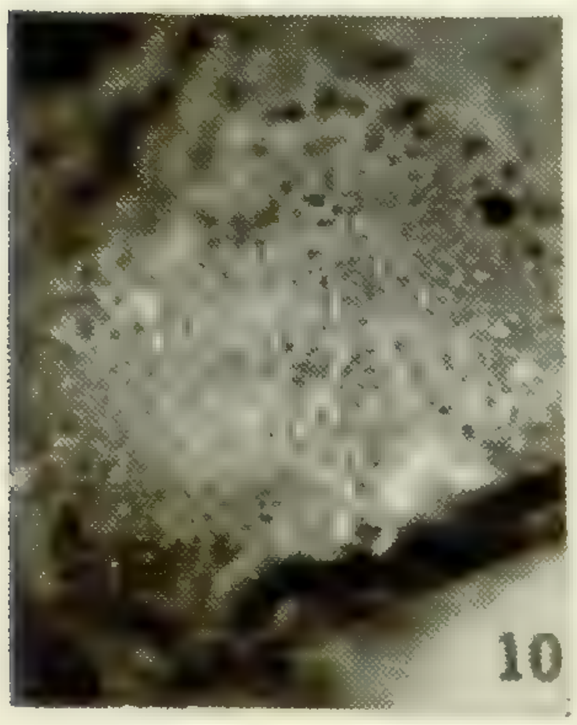
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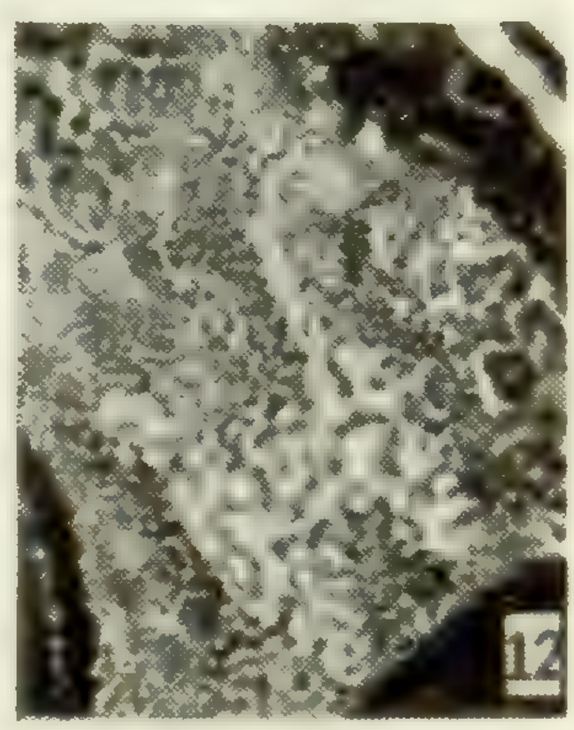
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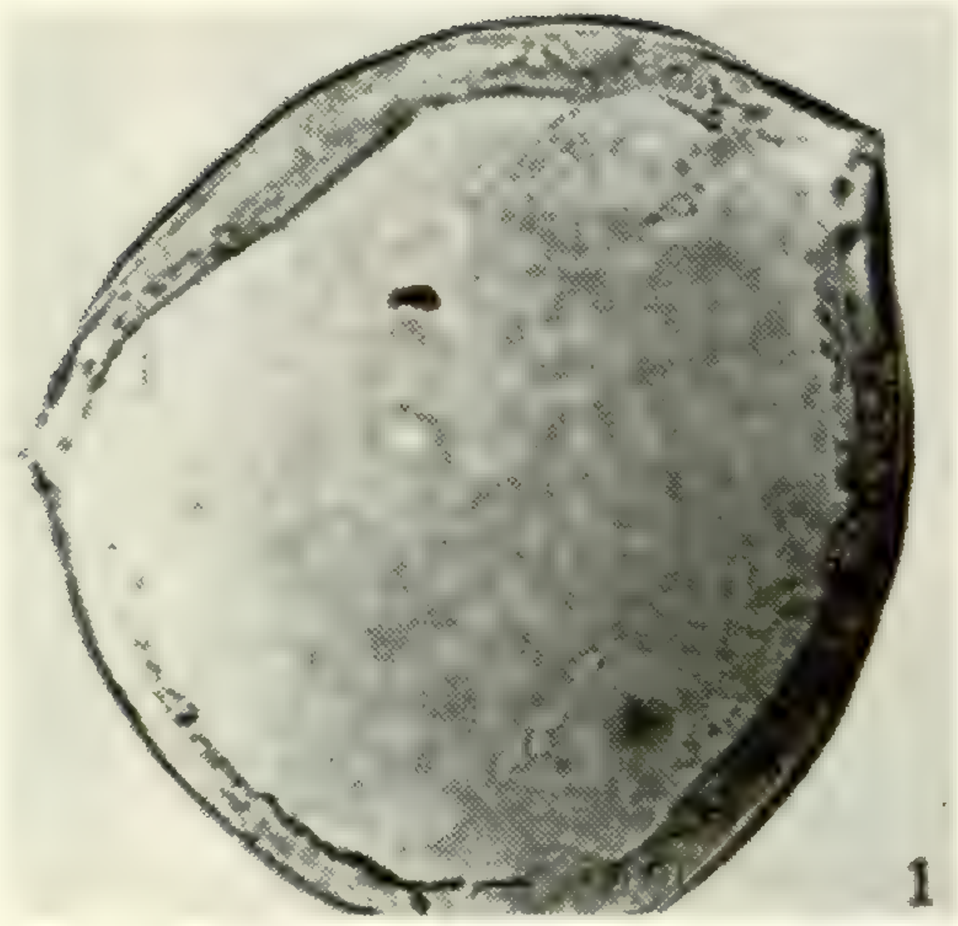
PLATE 22. FIG. 1. *Piptostigma multinervium* Engl. & Diels, × 500. FIG. 2,3. *P. glabrescens* Oliv., × 500. FIG. 4. *Xylopia densiflora* R. E. Fries, × 500. FIG. 5. *X. sericea* St. Hil., × 500. FIG. 6. *X. polyantha* R. E. Fries, × 500. FIG. 7,8. *X. discreta* (L.f.) Sprague & Hutchinson, × 1000. FIG. 9. *Fusaea decurrens* R. E. Fries, × 200. FIG. 10. *Cananga odorata* (Lam.) Hk.f. & Th., × 1000. FIG. 11,12. *Neostenanthera gabonensis* (Engl. & Diels) Exell; Fig. 11, × 500; Fig. 12, × 1000.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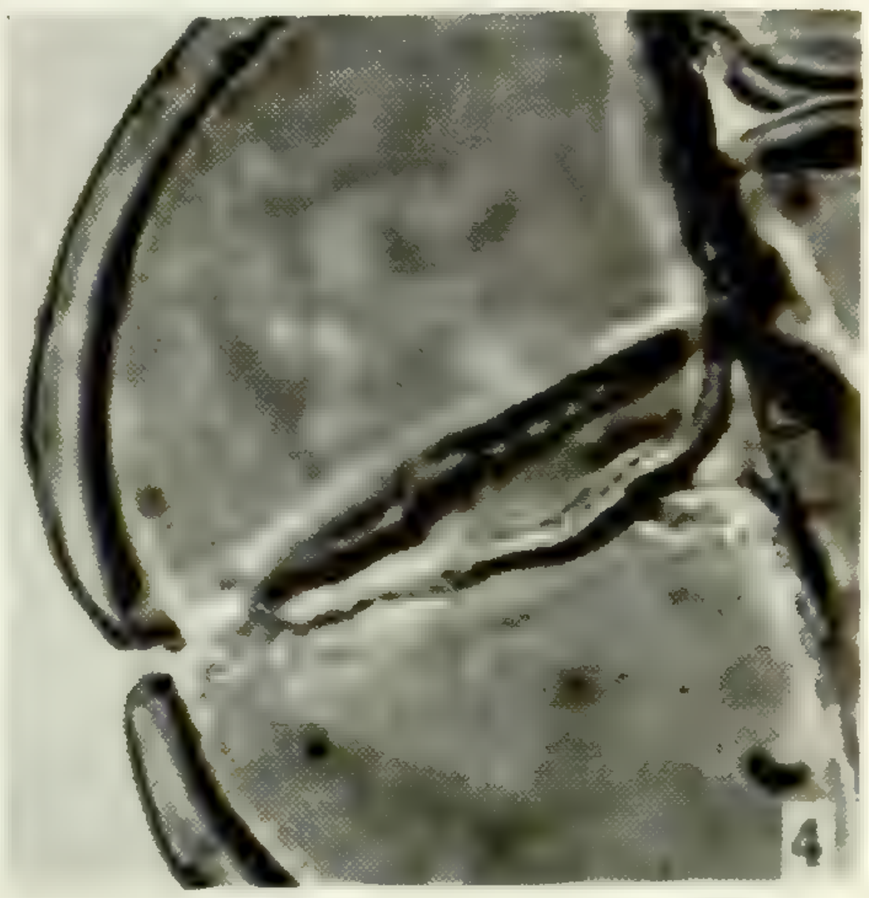
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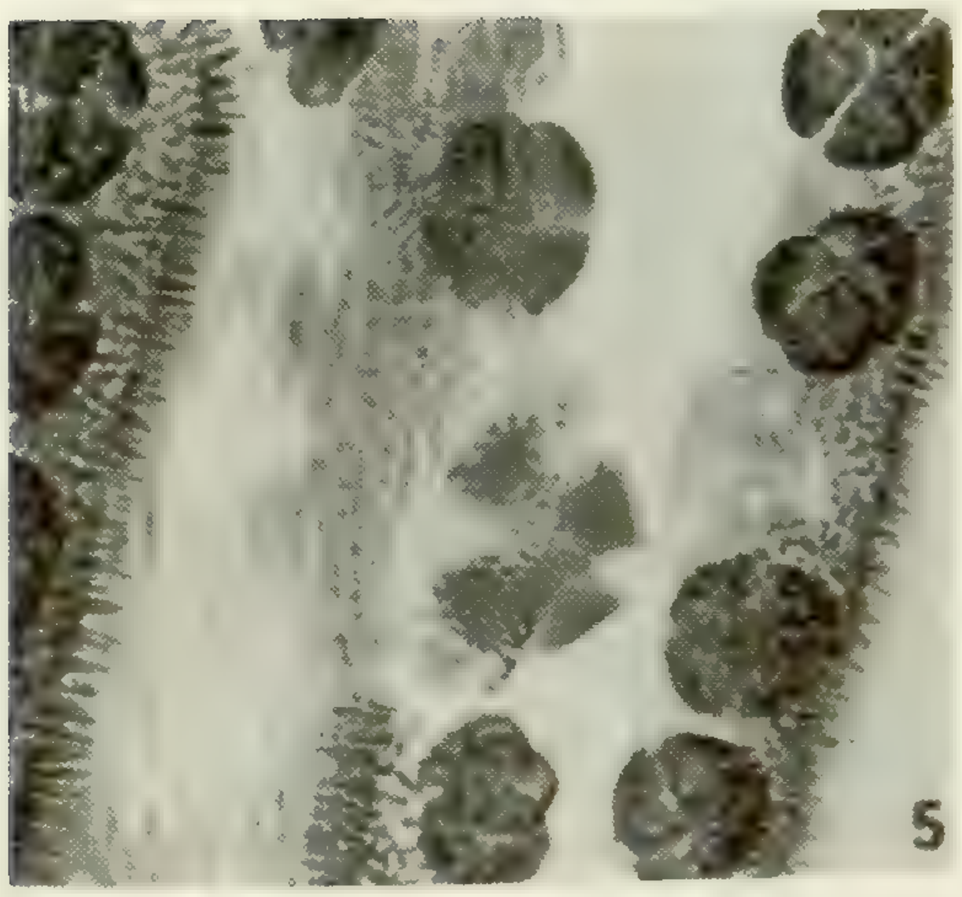
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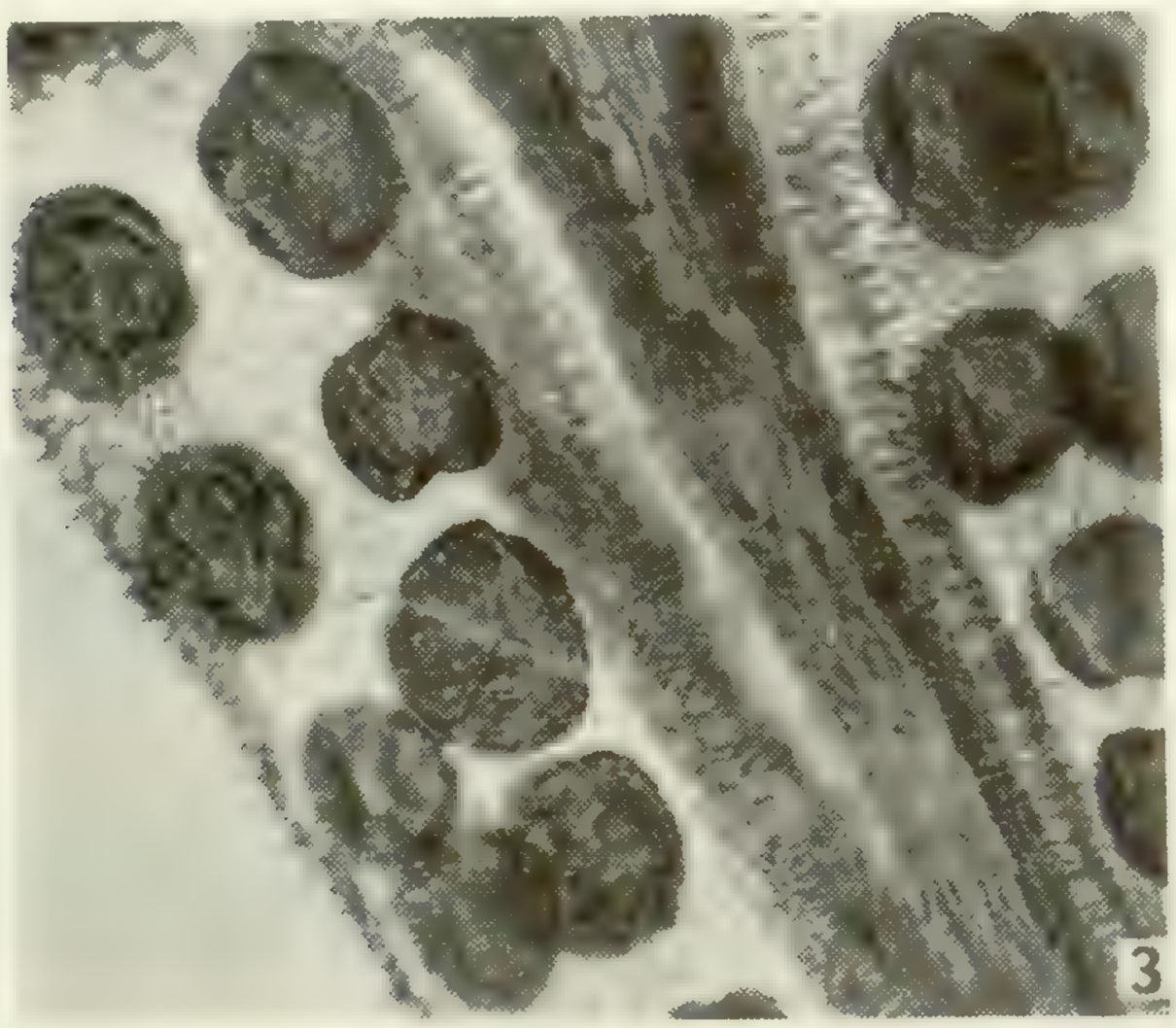
PLATE 23. FIG. 1. *Xylopia africana* (Benth.) Oliv., × 500. FIG. 2–4. *X. sericea* St. Hil.; Fig. 2,4, × 1000; Fig. 3, × 500. FIG. 5. *X. polyantha* R. E. Fries, × 200. FIG. 6. *X. brasiliensis* Spreng., × 200.



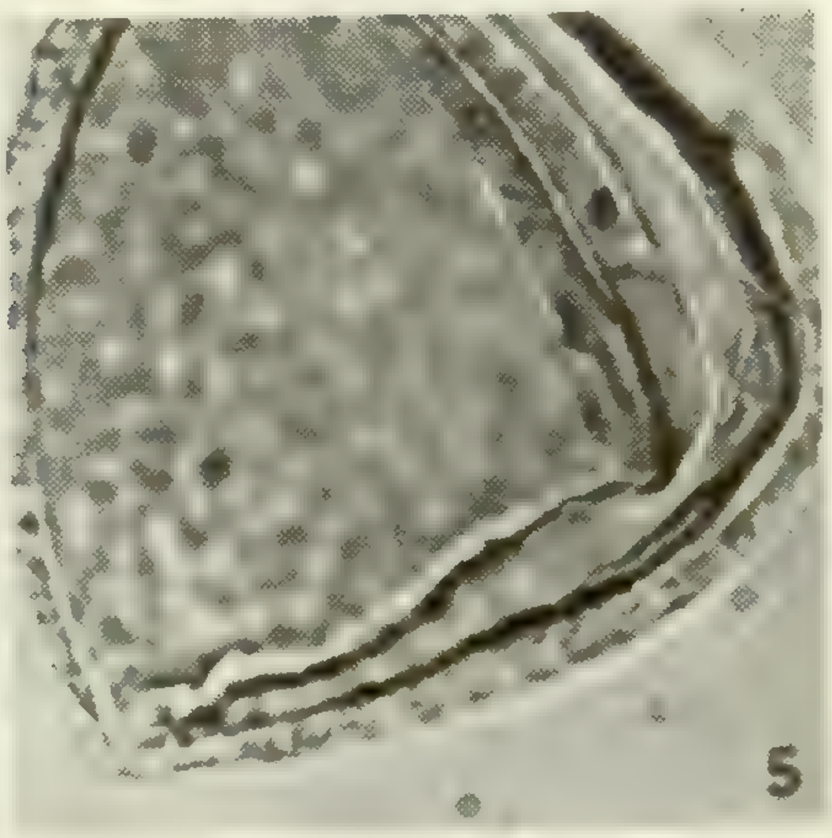
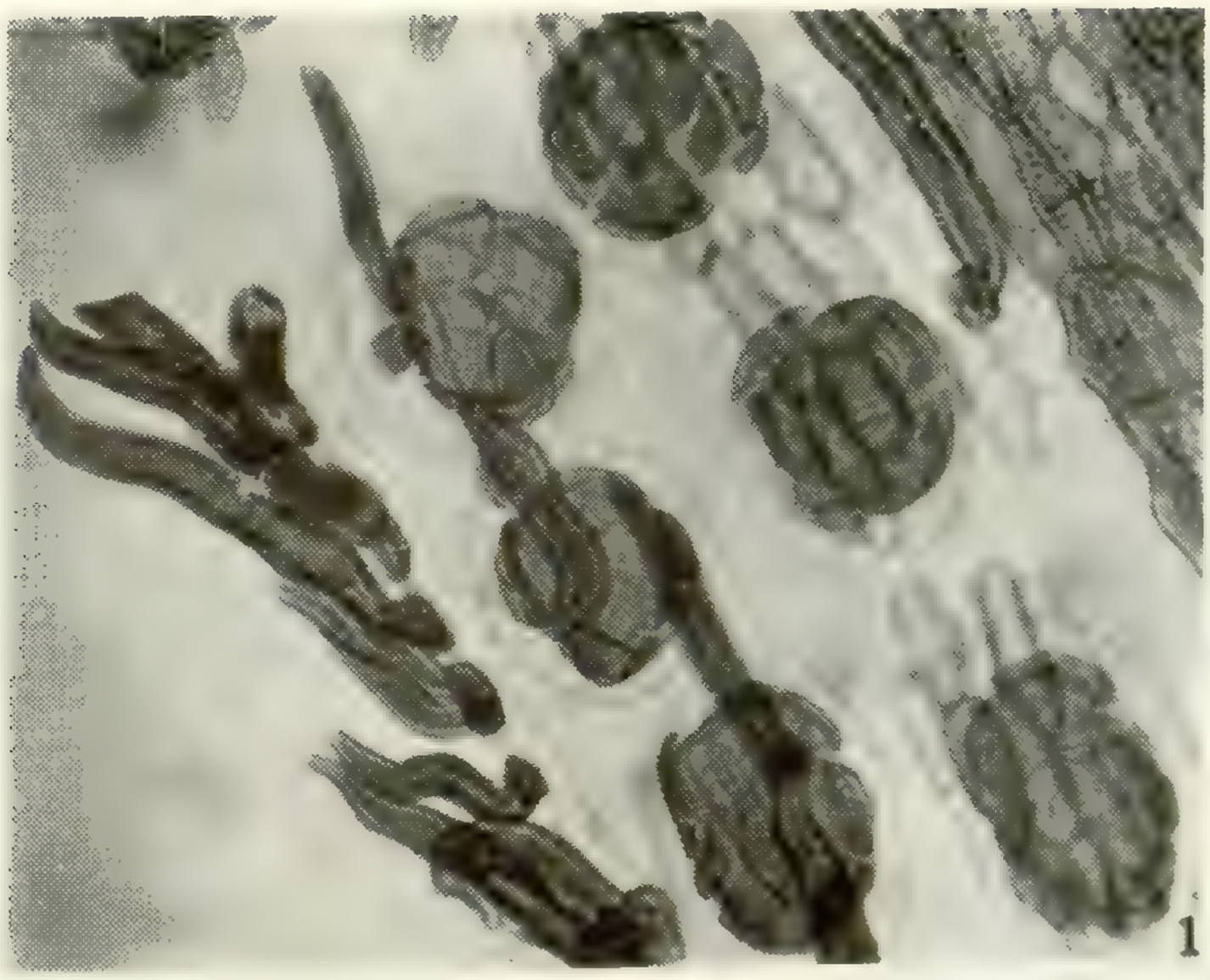


PLATE 24. FIG. 1,2. *Xylopia densiflora* R. E. Fries, × 1000. FIG. 3. *X. aromatica* (Lam.) Mart., × 200. FIG. 4,5. *X. polyantha* R. E. Fries, × 1000.



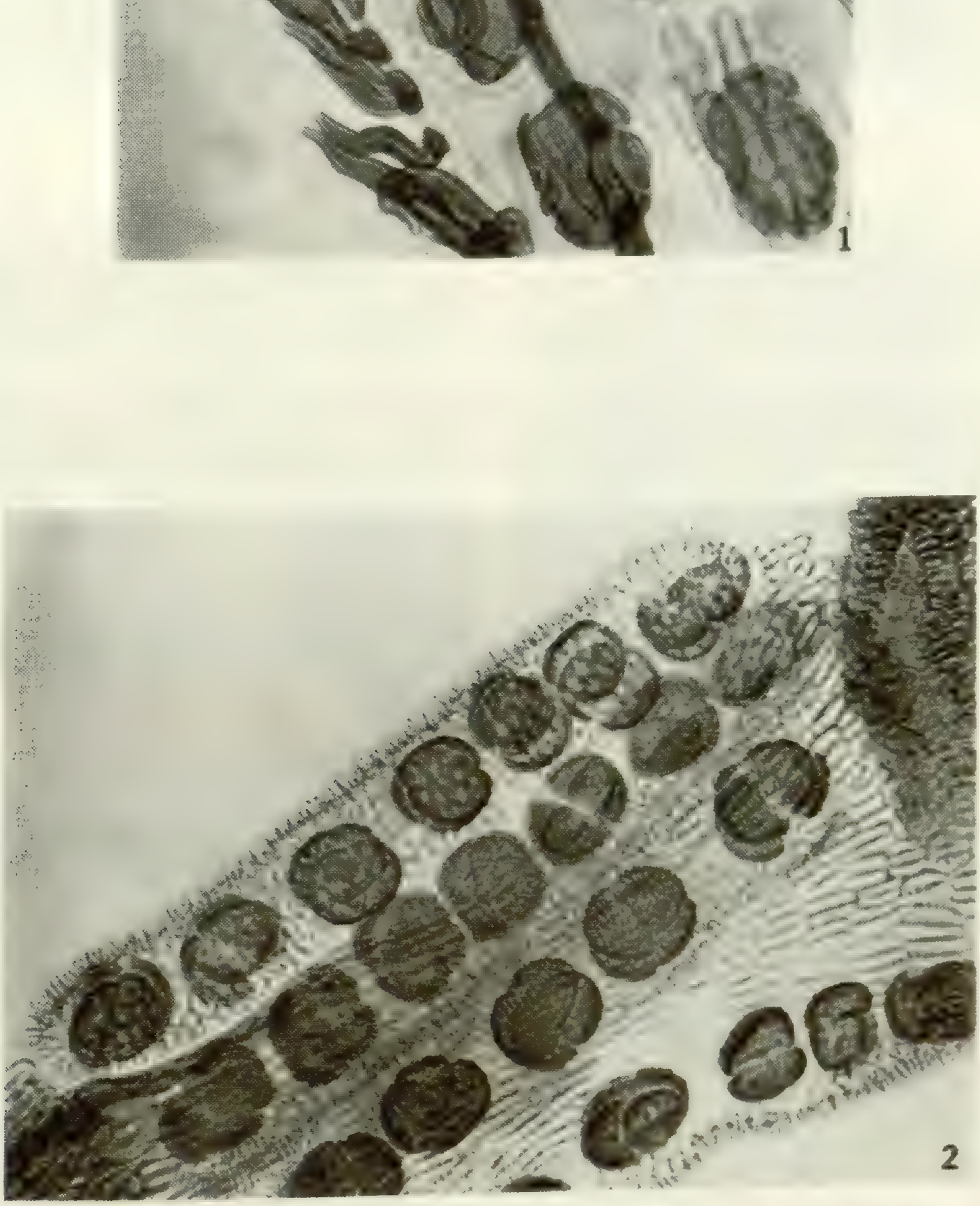
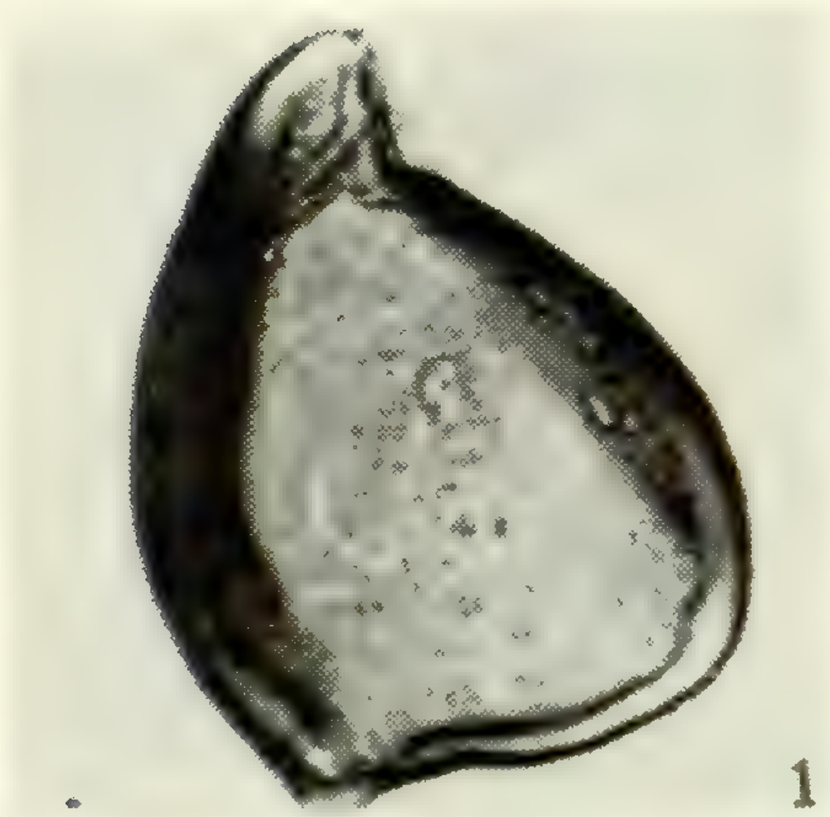


PLATE 25. FIG. 1. *Xylopia ferruginea* (Hk.f. & Th.) Hk.f. & Th., × 200. FIG. 2. *X. discreta* (L.f.) Sprague & Hutchinson, × 200.



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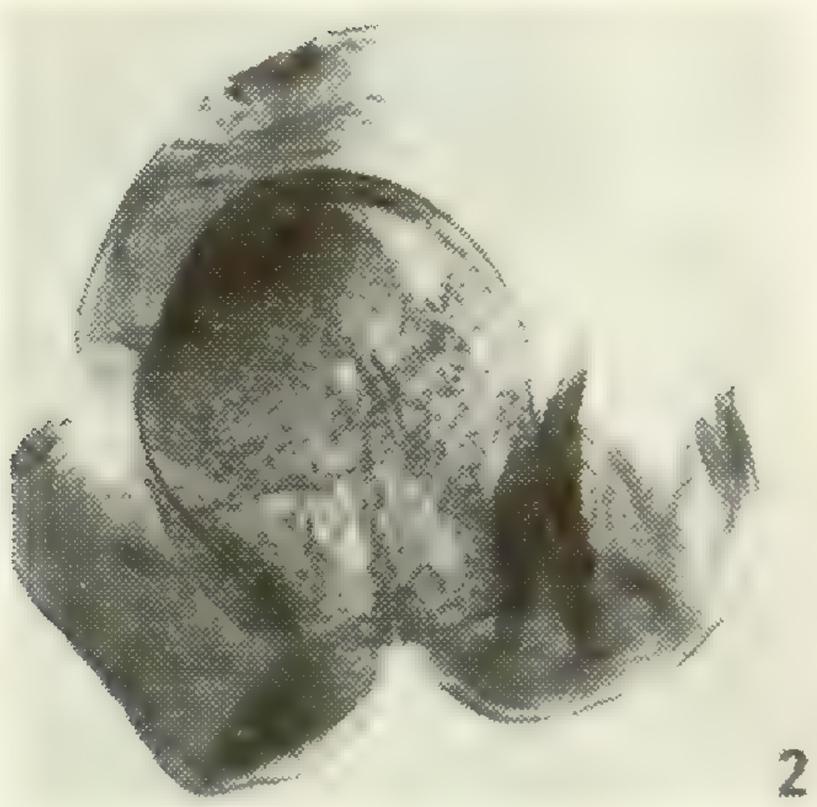

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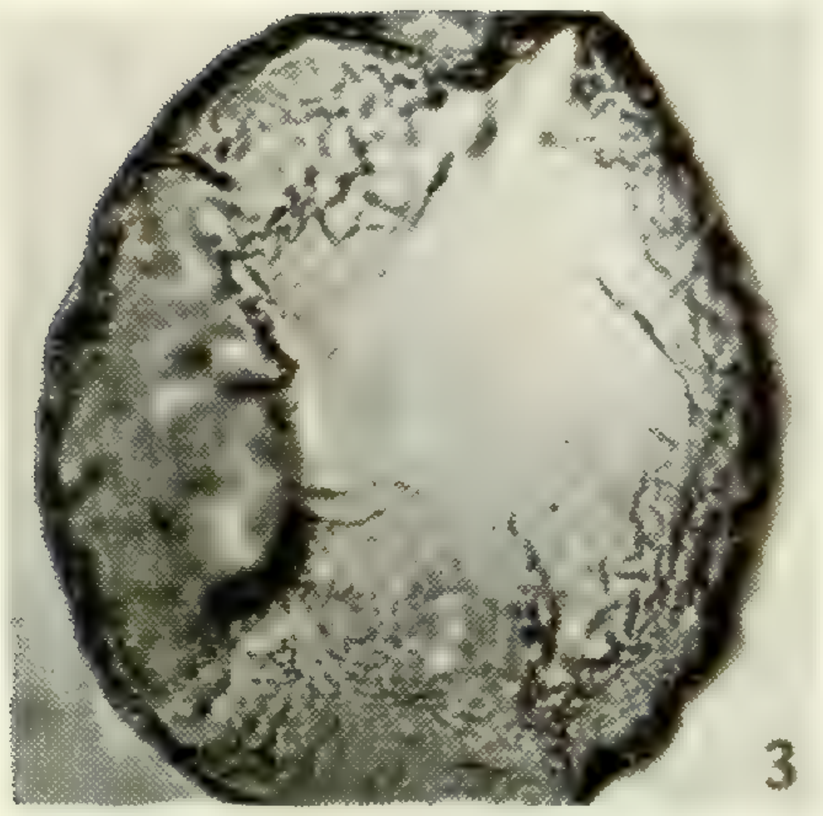

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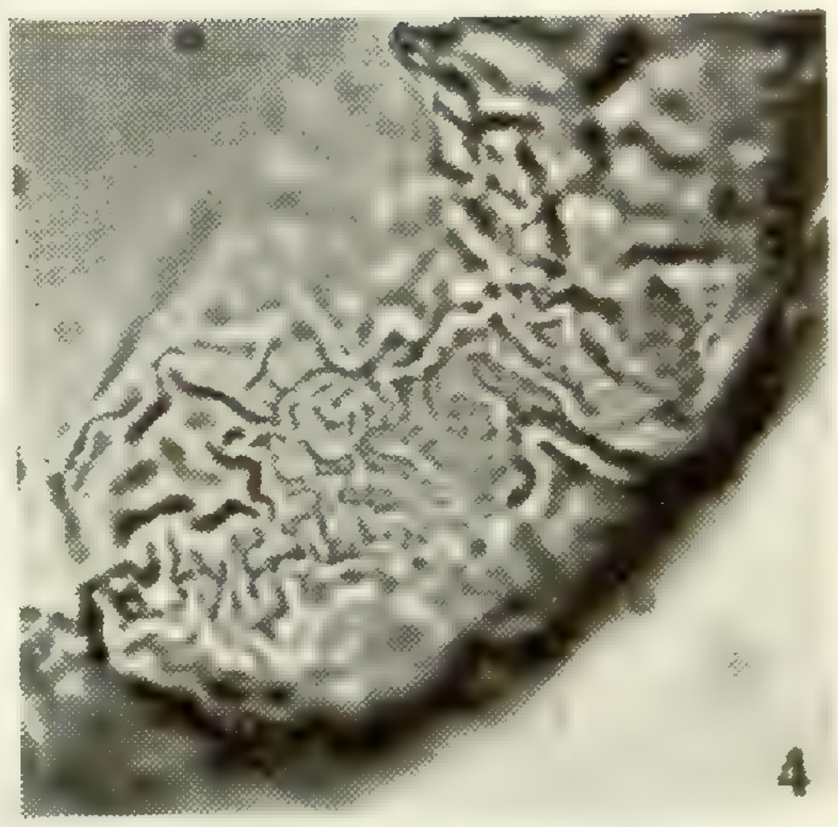

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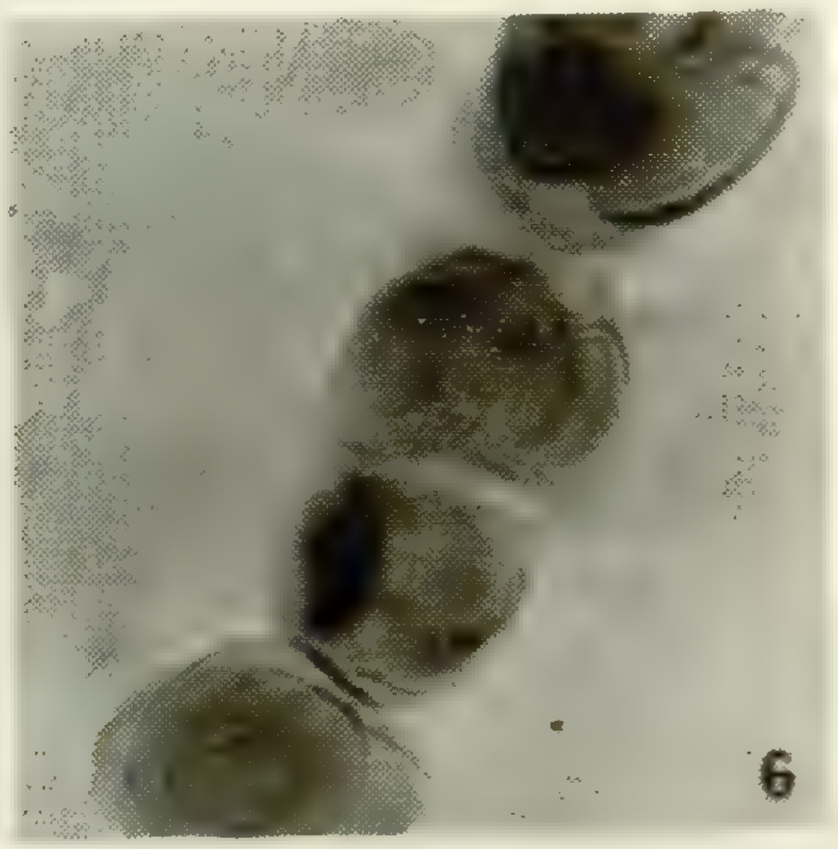
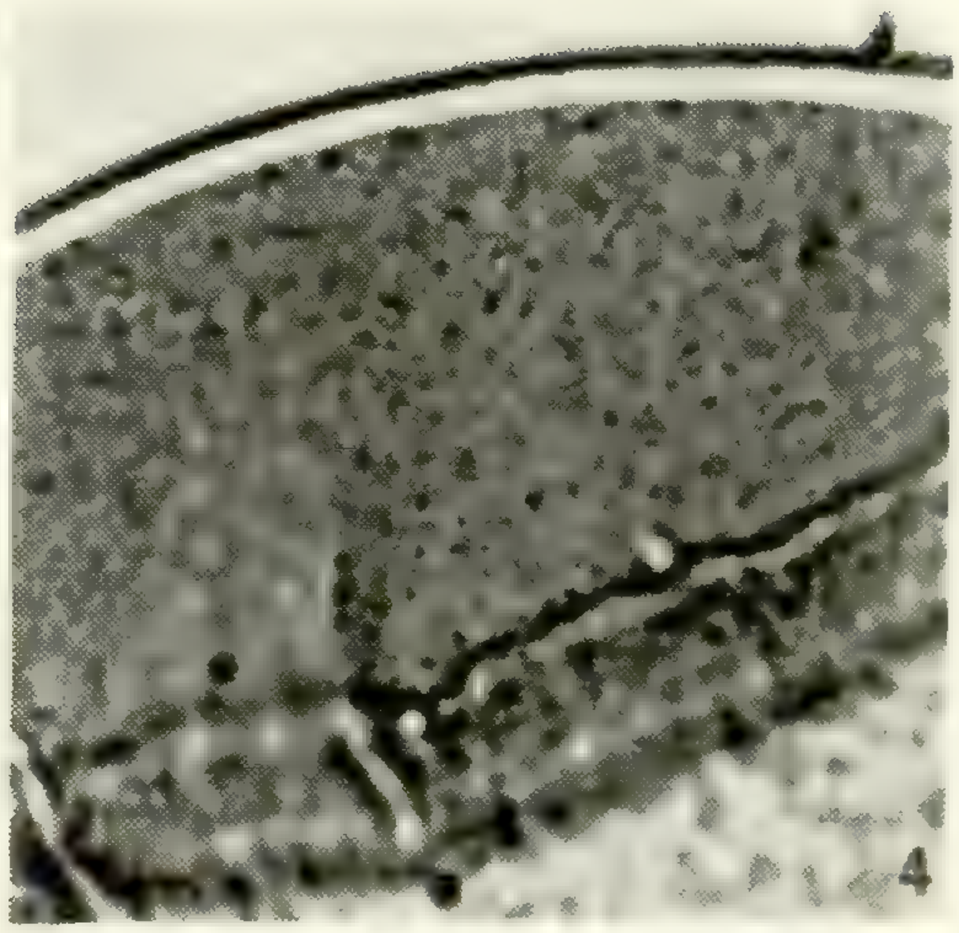


6

PLATE 26. FIG. 1. *Fusaea longifolia* (Aubl.) Saff., × 500. FIG. 2. *Duckeanthus grandiflorus* R. E. Fries, × 200. FIG. 3,4. *Cananga odorata* (Lam.) Hk.f. & Th.; Fig. 3, × 500; Fig. 4, × 1000. FIG. 5,6. *C. latifolia* (Hk.f. & Th.) Finet & Gagnep.; Fig. 5, × 500; Fig. 6, × 200.

1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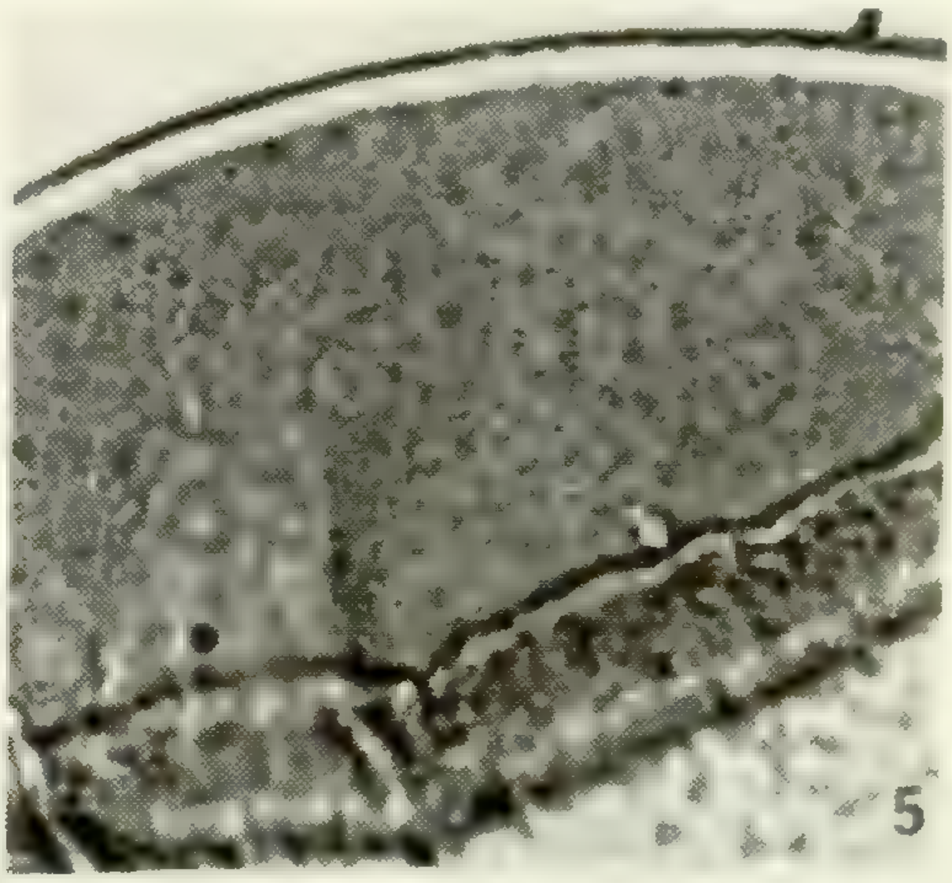
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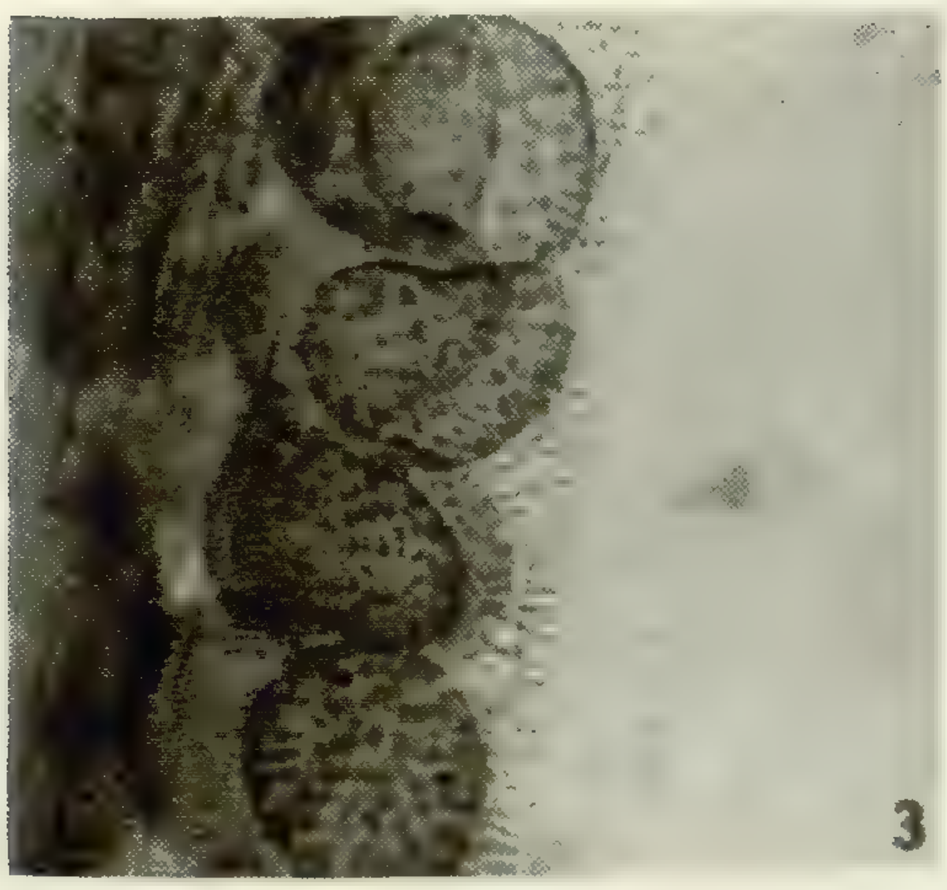
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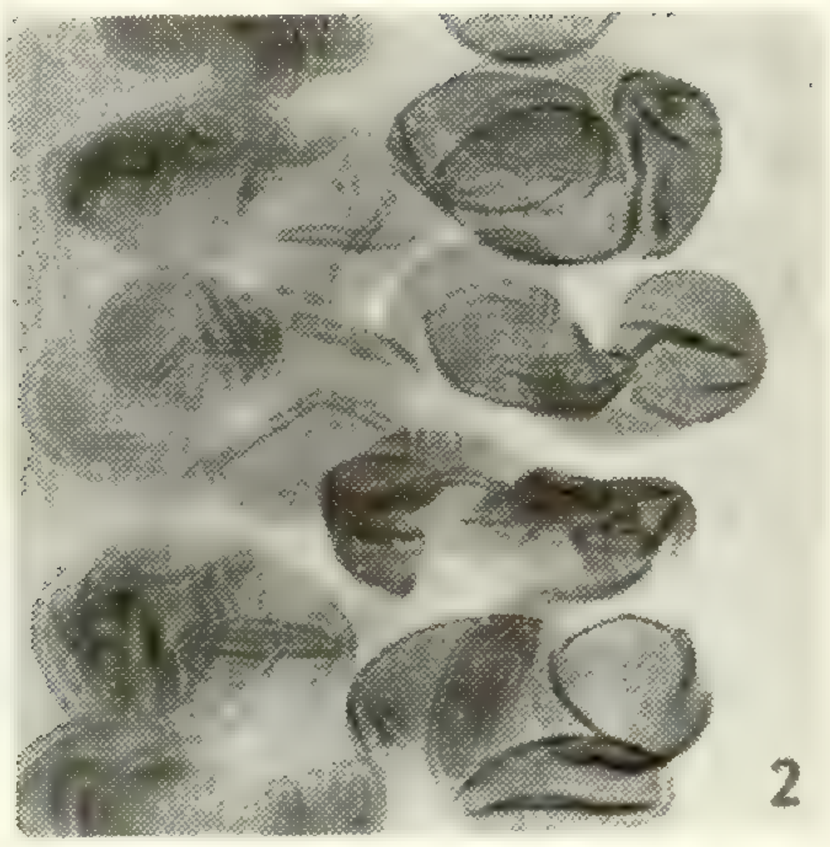
PLATE 27. FIG. 1. *Fusaea decurrens* R. E. Fries, × 500. FIG. 2. *Duckeanthus grandiflorus* R. E. Fries, × 1000. FIG. 3. *Cananga odorata* (Lam.) Hk.f. & Th., × 200. FIG. 4–6. *C. latifolia* (Hk.f. & Th.) Finet & Gagnep., × 1000.

1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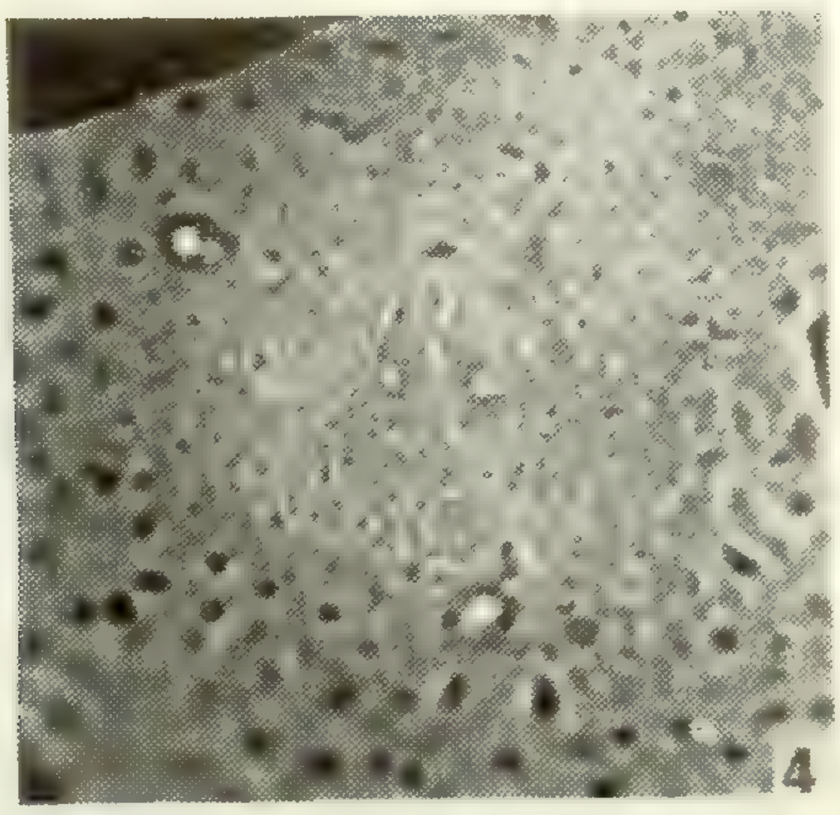
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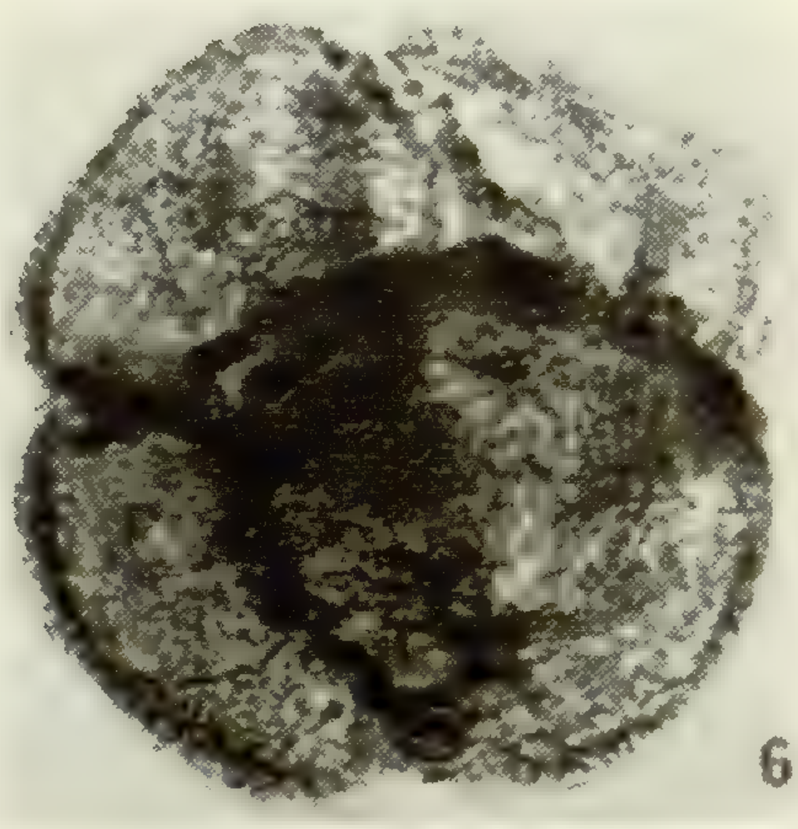
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PLATE 28. FIG. 1. *Meiocarpidium lepidotum* (Oliv.) Engl. & Diels, × 500. FIG. 2. *Goniothalamus puncticulifolius* Merr., × 200. FIG. 3. *G. grandiflorus* (Warb.) Boerl., × 500. FIG. 4. *G. chartaceus* Li, × 1000. FIG. 5. *G. curtisii* King, × 500. FIG. 6. *Monodora junodii* Engl. & Diels, × 500.

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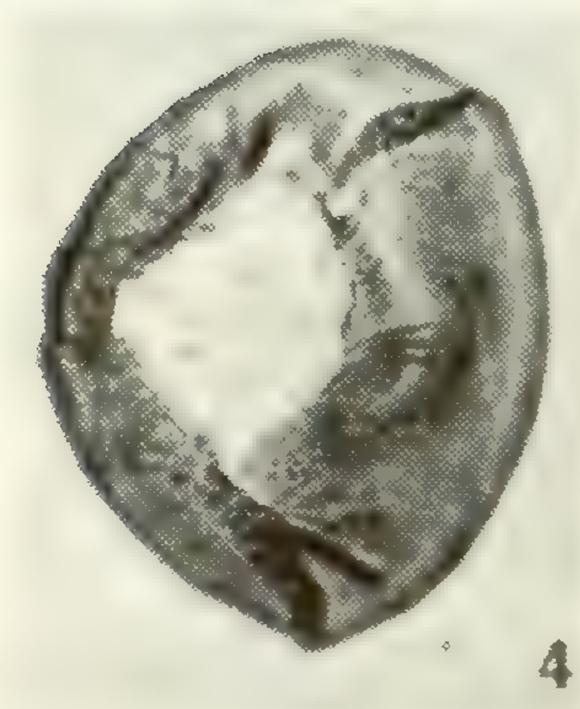
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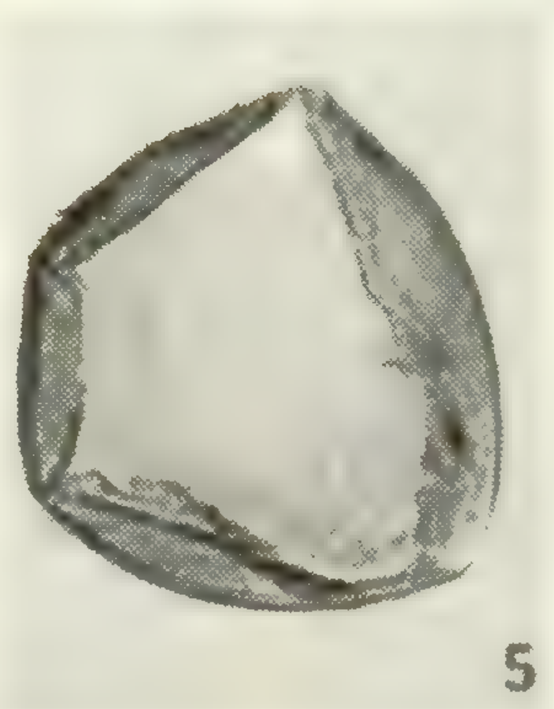
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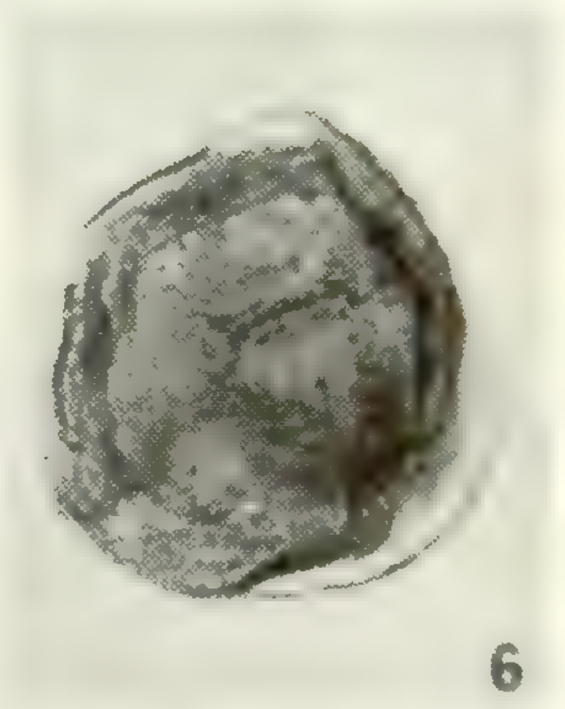
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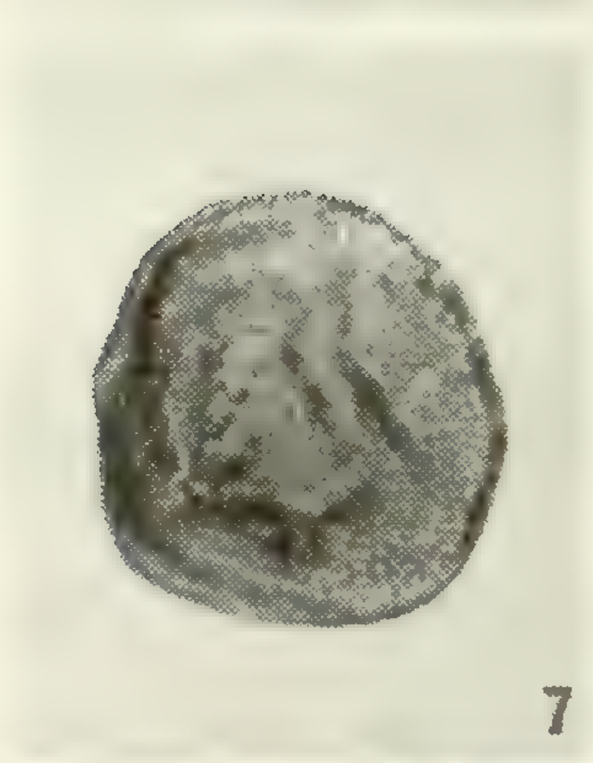
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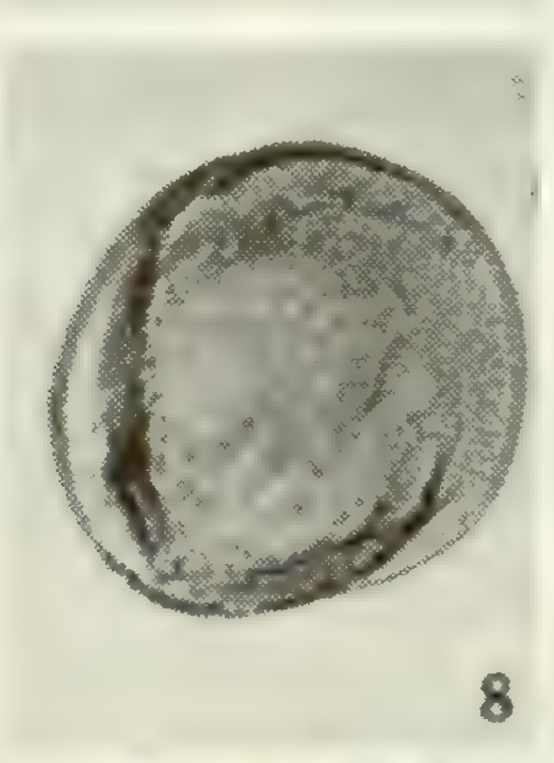
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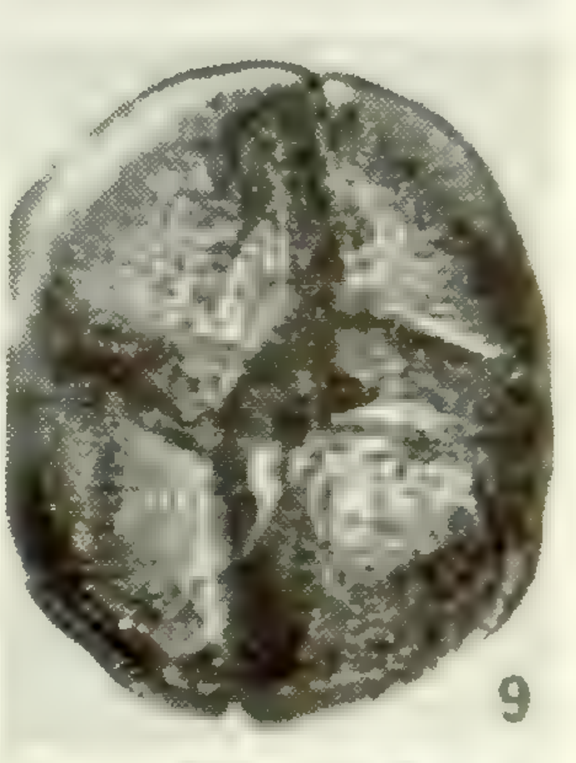
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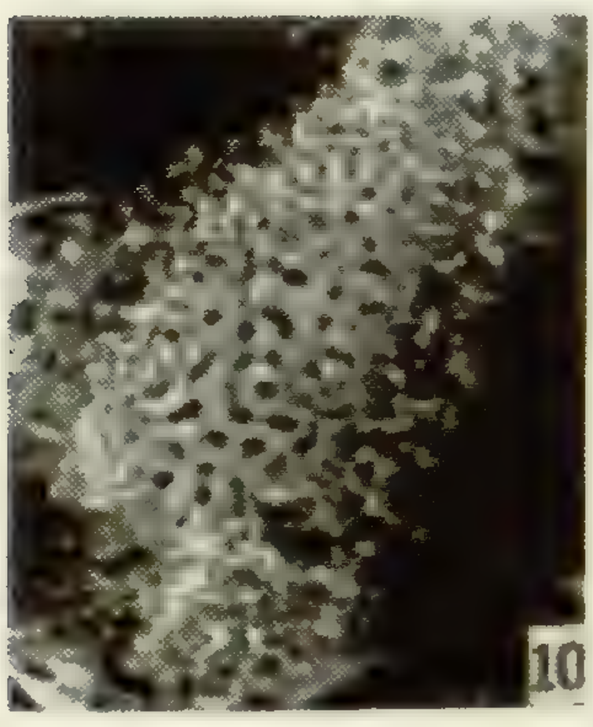
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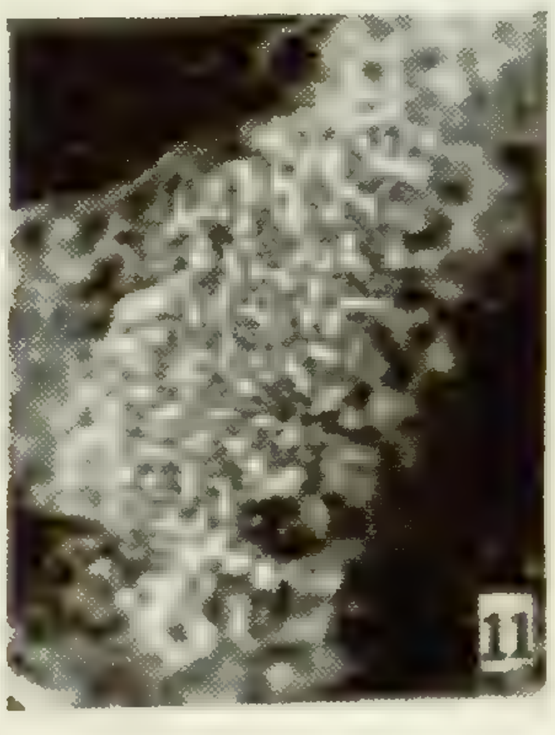
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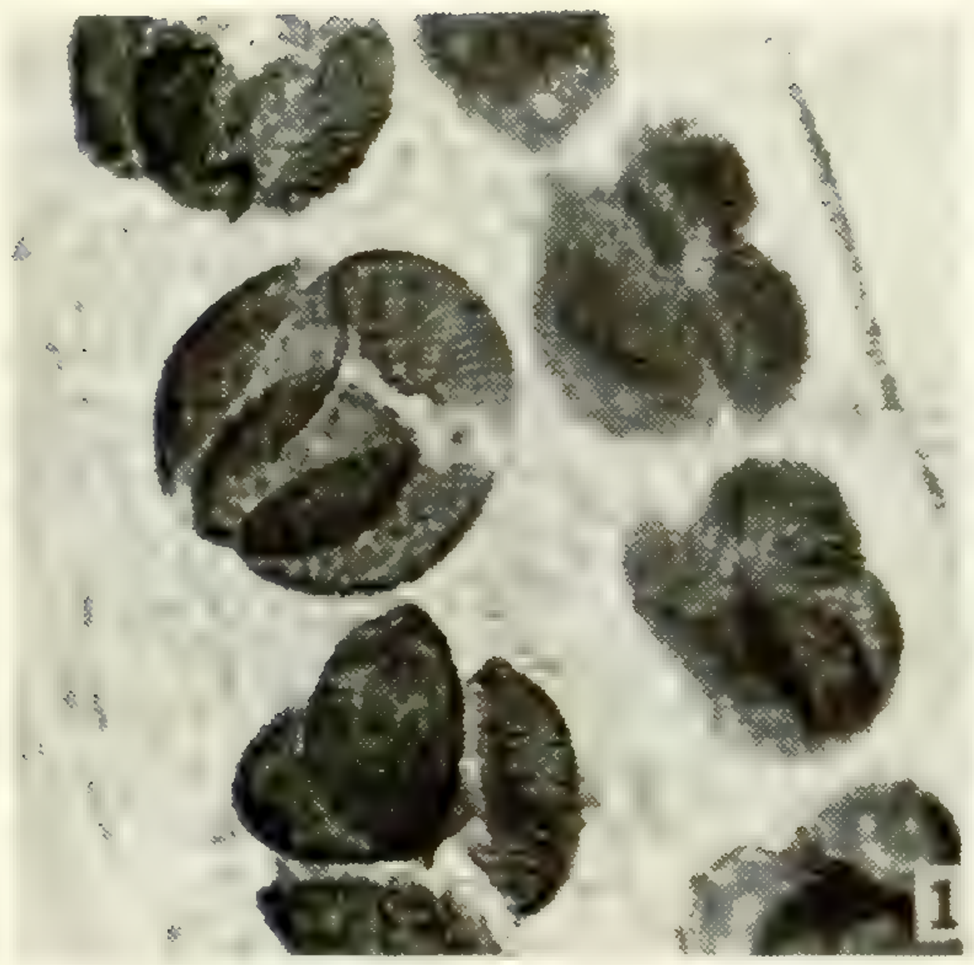
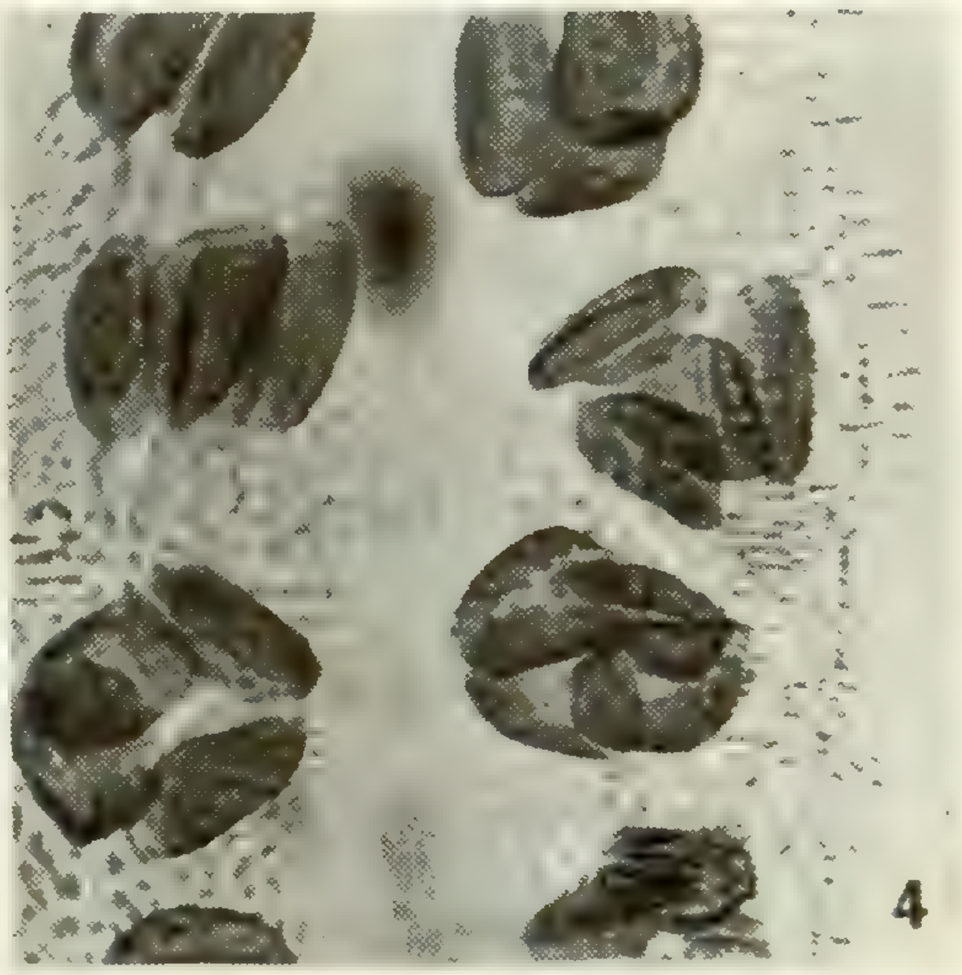
PLATE 29. FIG. 1. *Neostenanthera myristicifolia* (Oliv.) Exell, × 500. FIG. 2. *Goniothalamus saigonensis* Pierre ex Finet & Gagnep., × 500. FIG. 3. *G. velutinus* Airy-Shaw, × 500. FIG. 4. *G. puncticulifolius* Merr., × 500. FIG. 5. *Richella monosperma* A. Gray, × 500. FIG. 6. *Isolona congolana* (De Wild. & Th. Dur.) Engl. & Diels, × 500. FIG. 7. *I. pilosa* Diels, × 500. FIG. 8. *I. campanulata* Engl. & Diels, × 500. FIG. 9. *Uvariastrum pierreanum* Engl., × 500. FIG. 10–12. *U. zenkeri* Engl. & Diels, × 1000.





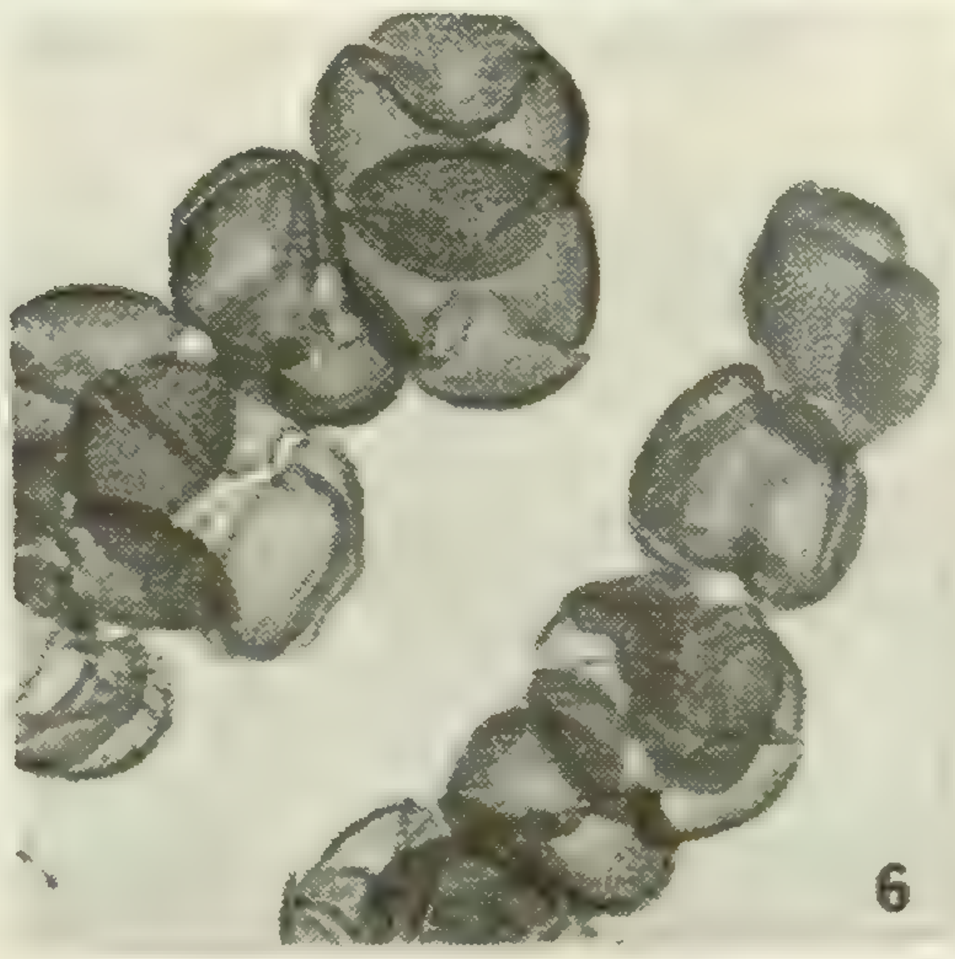
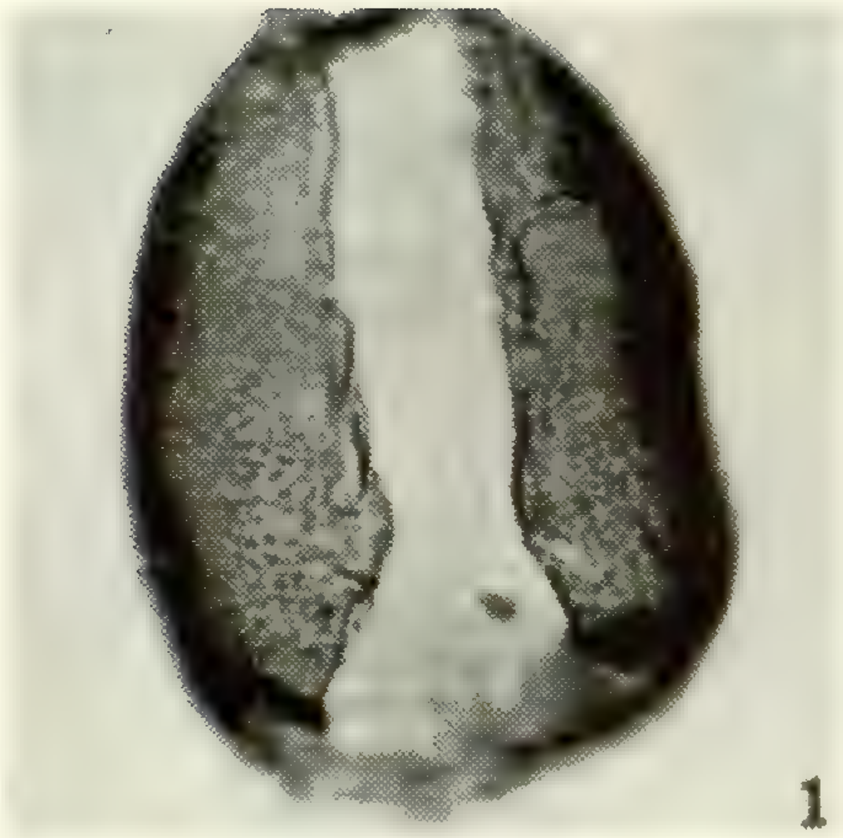


PLATE 30. FIG. 1. *Goniothalamus velutinus* Airy-Shaw, × 200. FIG. 2. *G. curtisii* King, × 200. FIG. 3. *G. puncticulifolius* Merr., × 500. FIG. 4. *Richella monosperma* A. Gray, × 200. FIG. 5. *Diclinanona calycina* (Diels) R. E. Fries, × 500. FIG. 6. *Asimina triloba* (L.) Dunal, × 200.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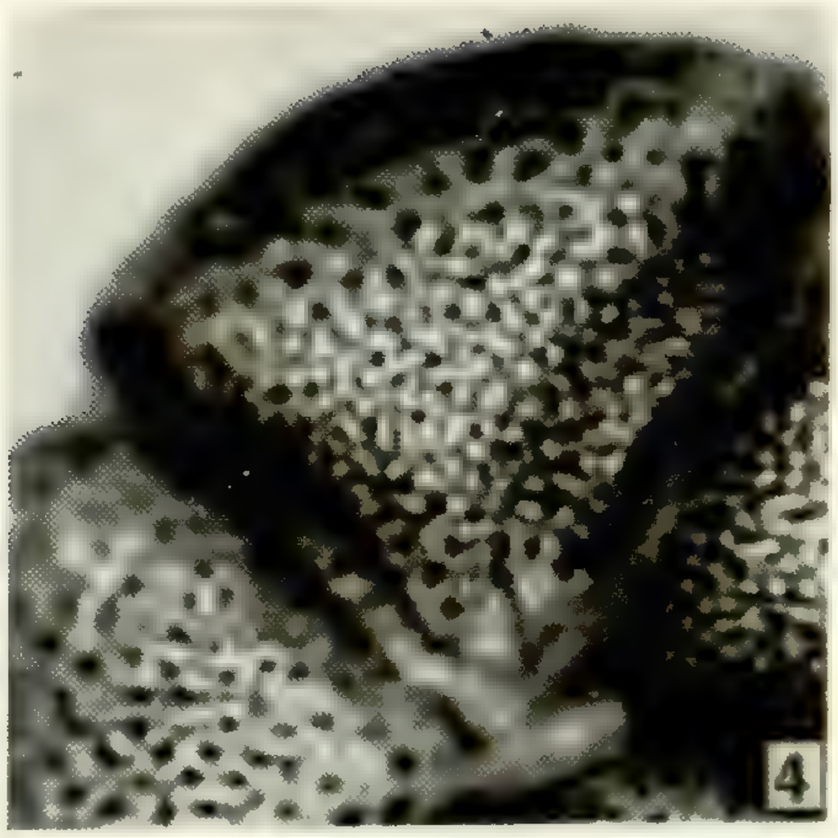
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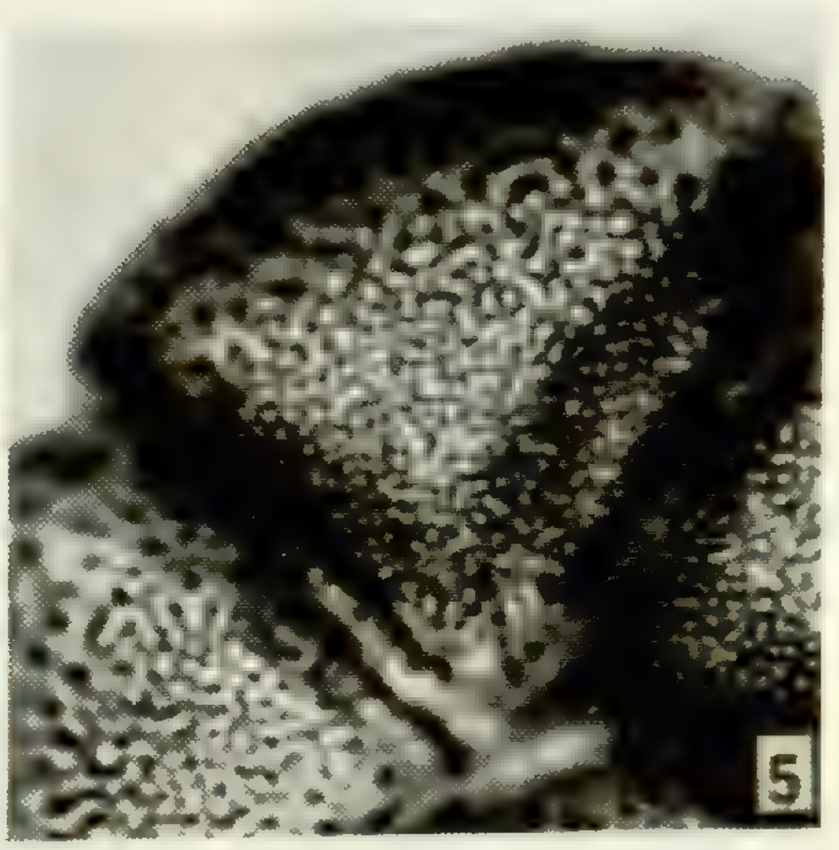
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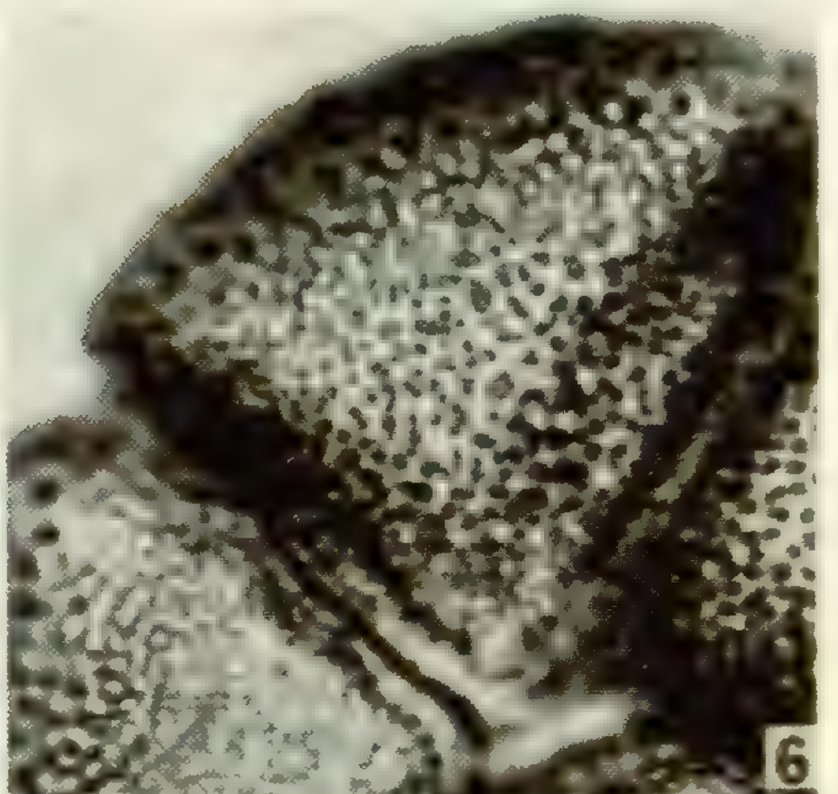
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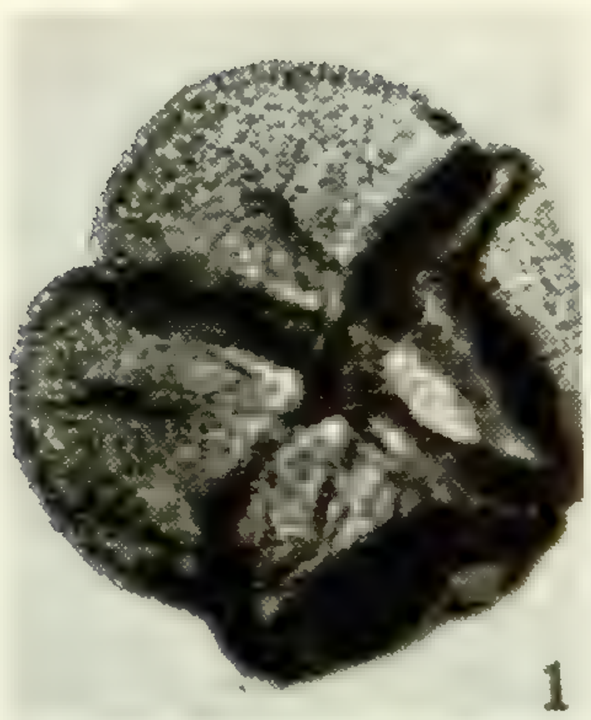
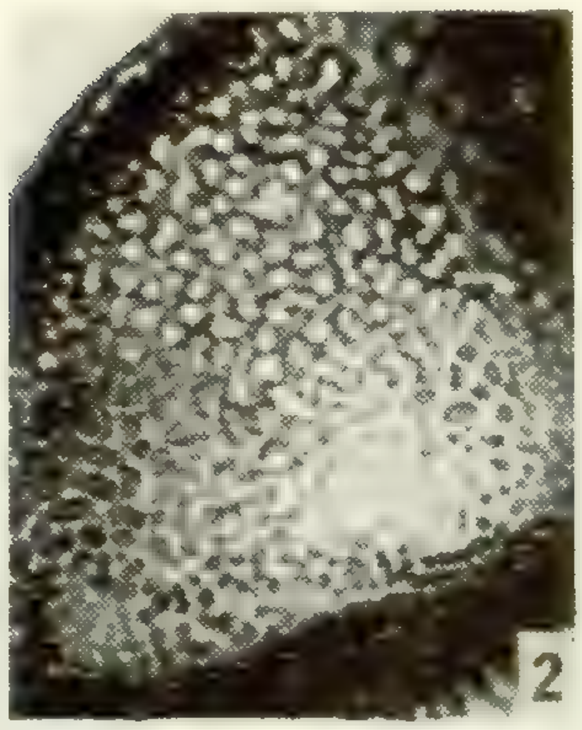
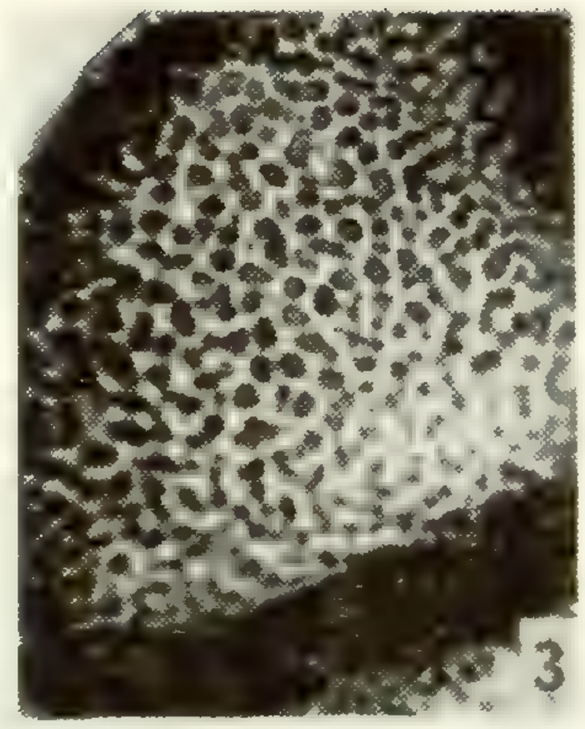
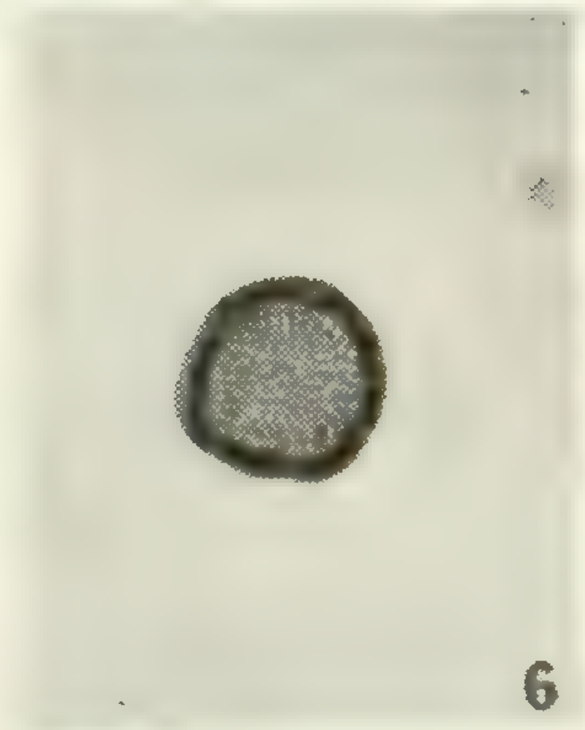
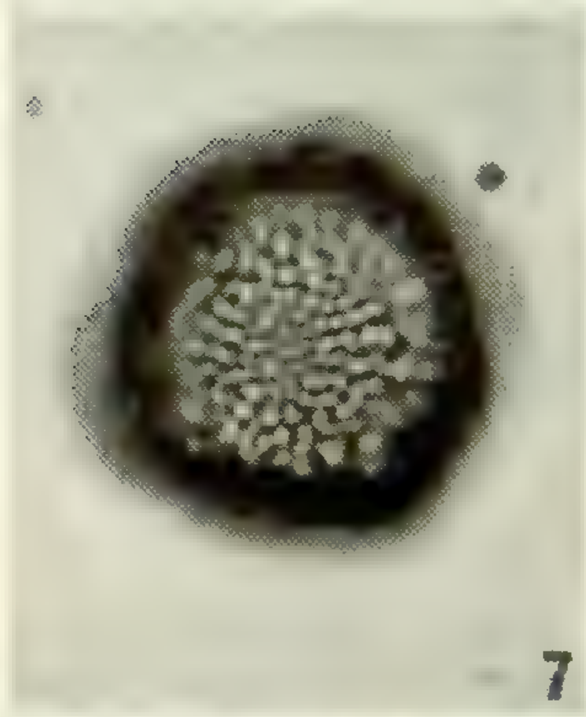
PLATE 31. FIG. 1. *Monodora tenuifolia* Benth., × 500. FIG. 2. *Uvariastrum hexalobioides* (R. E. Fries) R. E. Fries, × 500. FIG. 3. *Uvariopsis guineensis* Keay, × 500. FIG. 4–6. *Hexalobus monopetalus* (A. Rich.) Engl. & Diels, × 1000.

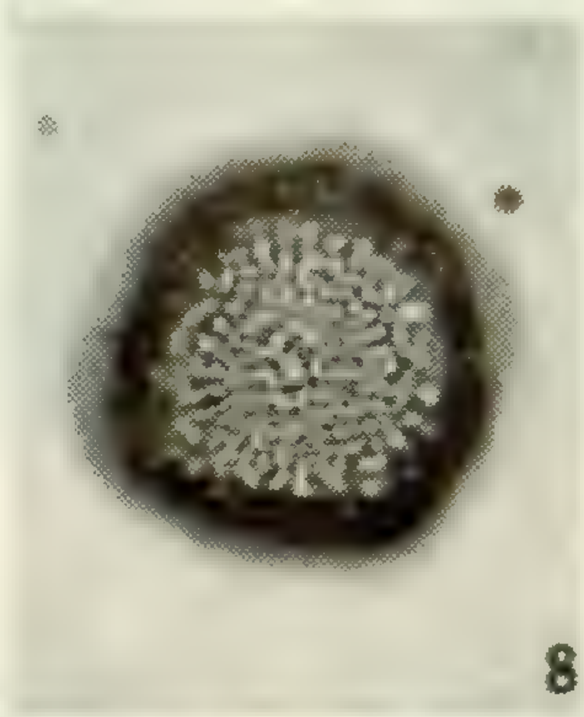


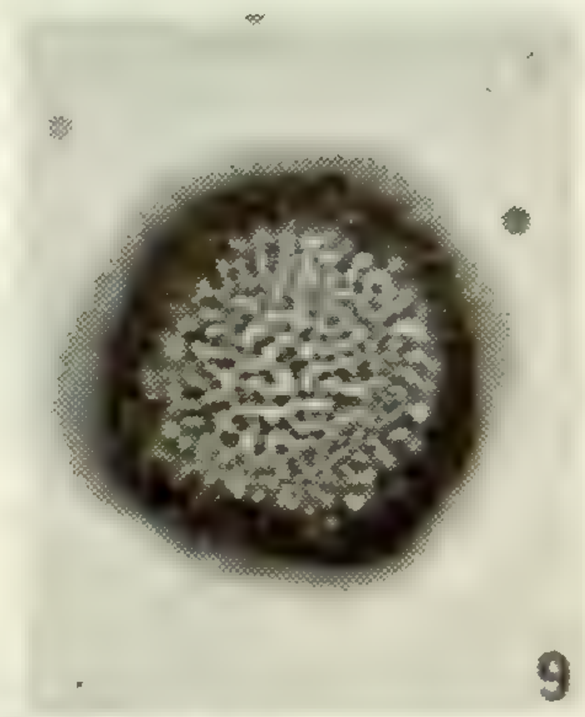


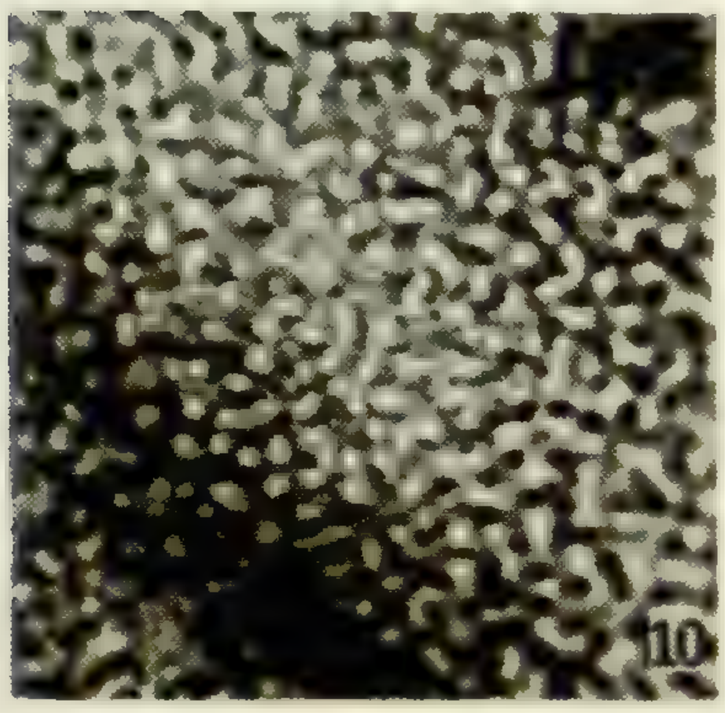












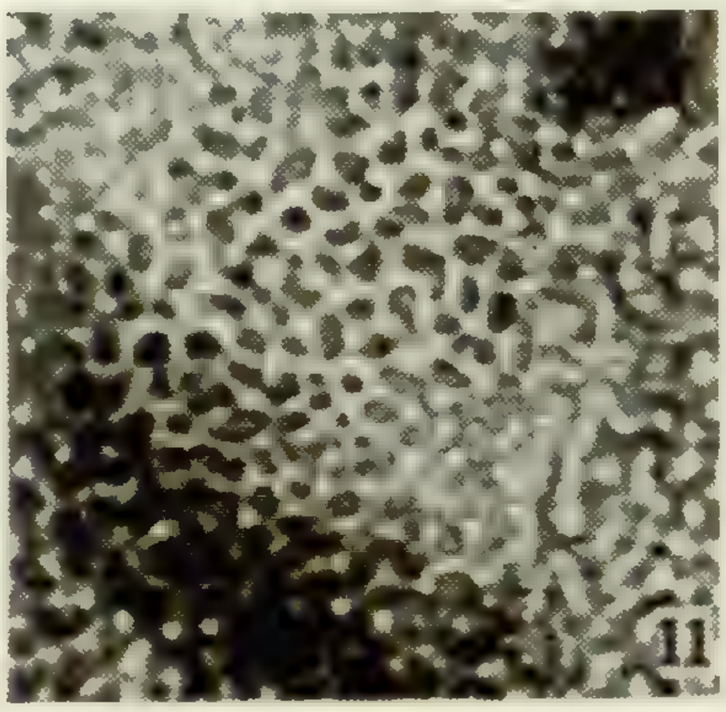
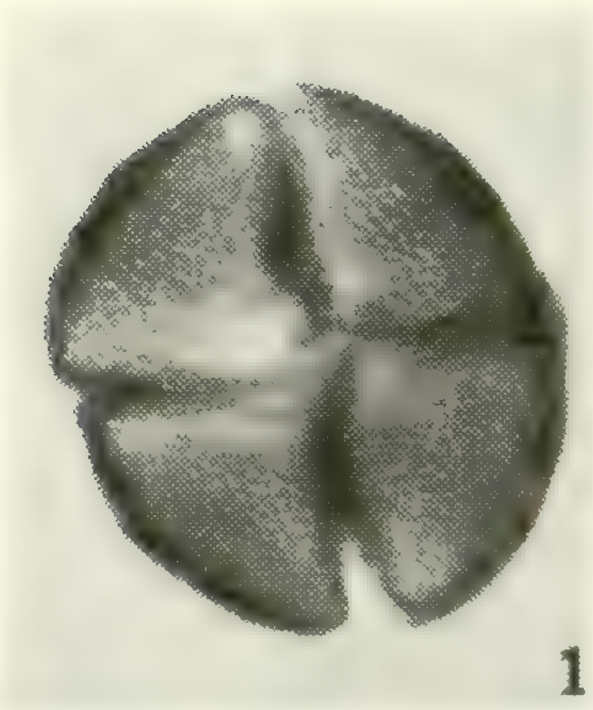
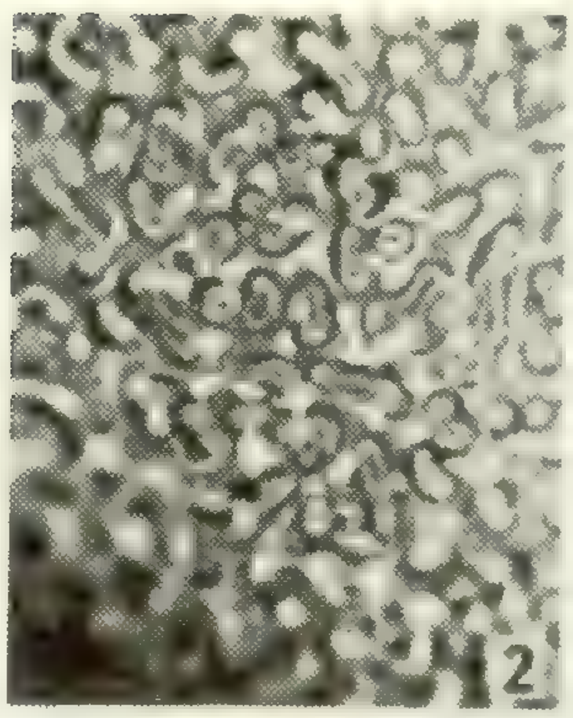
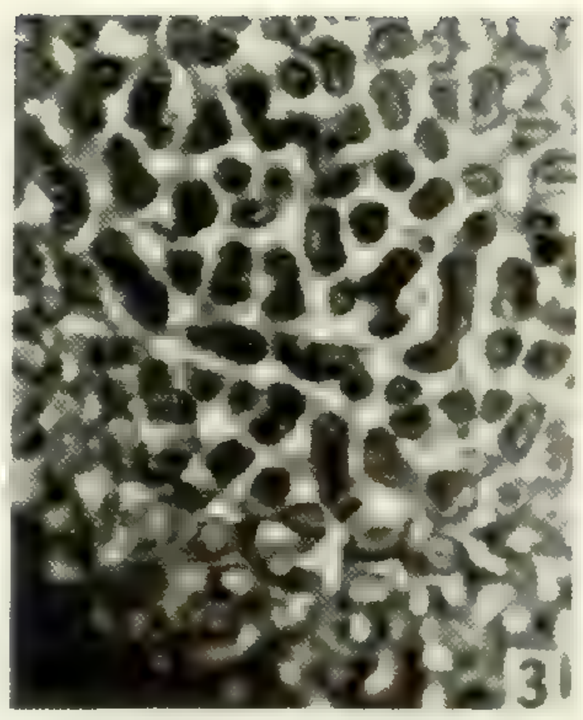
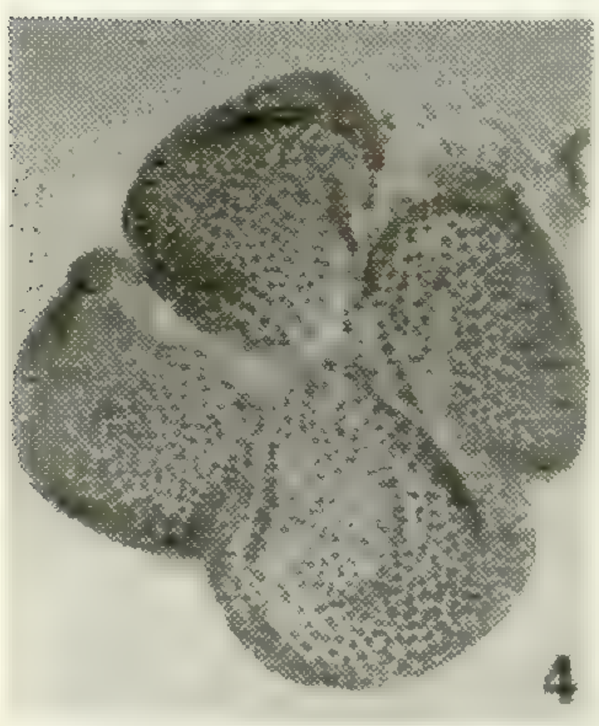


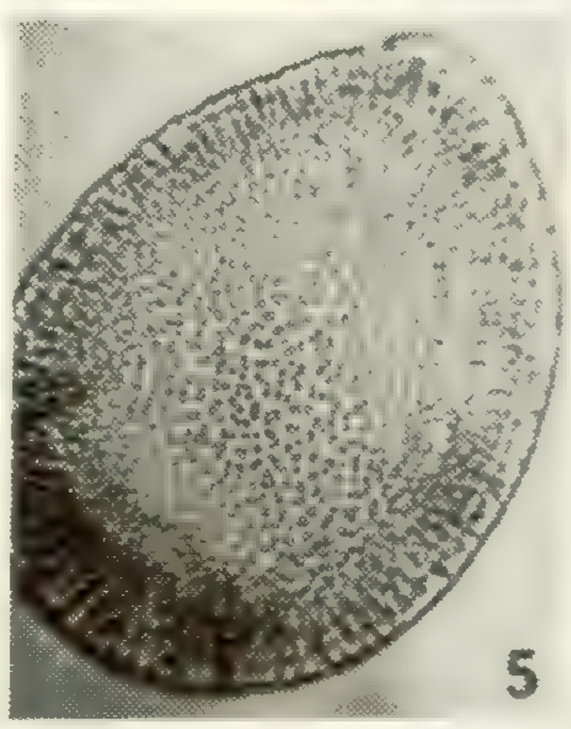
PLATE 32. FIG. 1. *Uvariopsis zenkeri* Engl., × 500. FIG. 2,3. *U. guineensis* Keay, × 1000. FIG. 4,5. *Hexalobus monopetalus* (A. Rich.) Engl. & Diels, × 500. FIG. 6–9. *Cleistochlamys kirkii* (Benth.) Oliv.; Fig. 6, × 500; Fig. 7,8,9, × 1000. FIG. 10,11. *Diclinanona calycina* (Diels) R. E. Fries, × 1000.

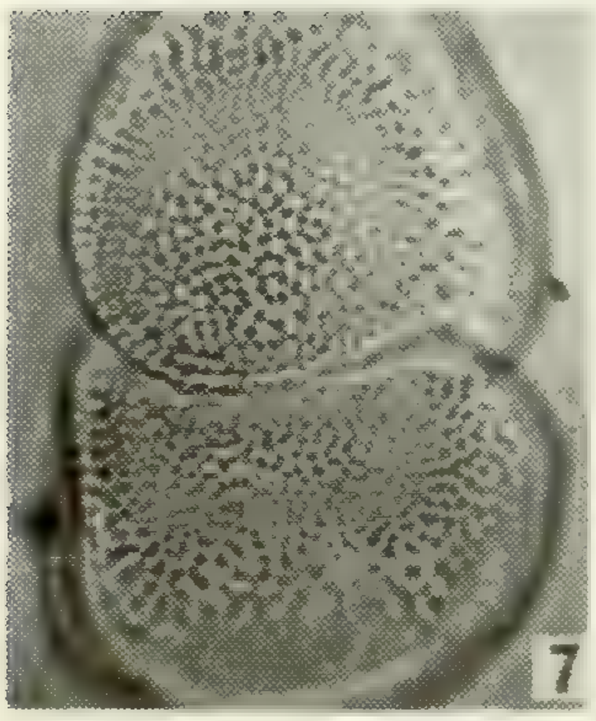


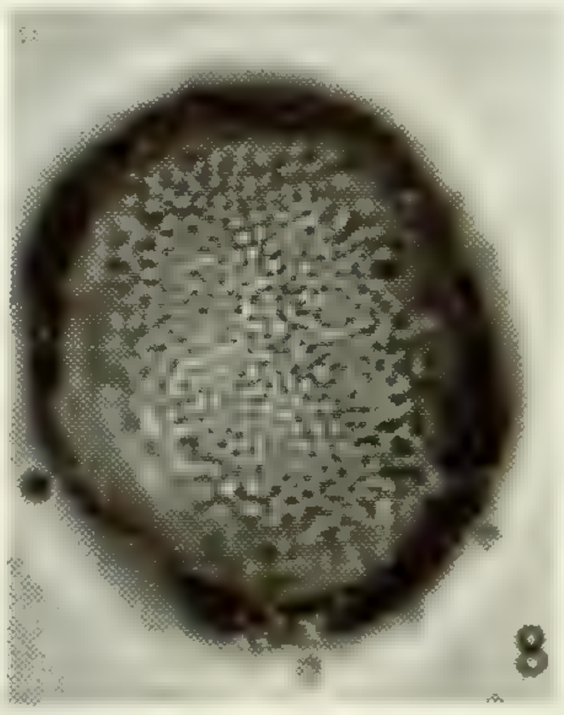


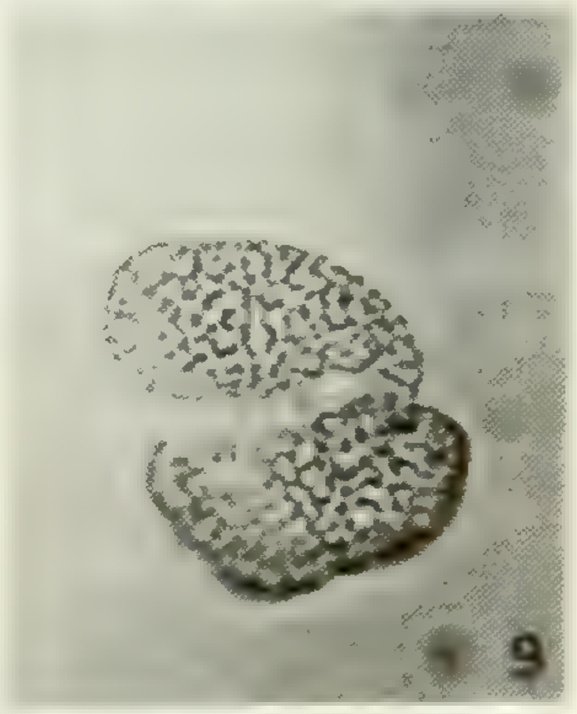


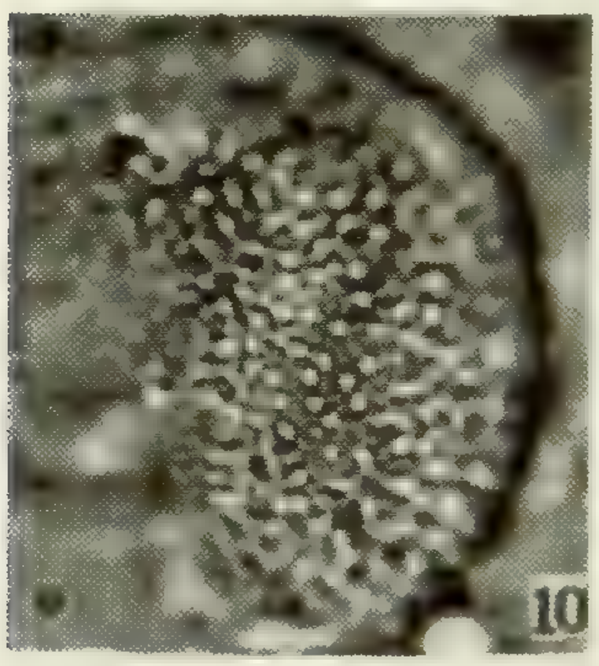


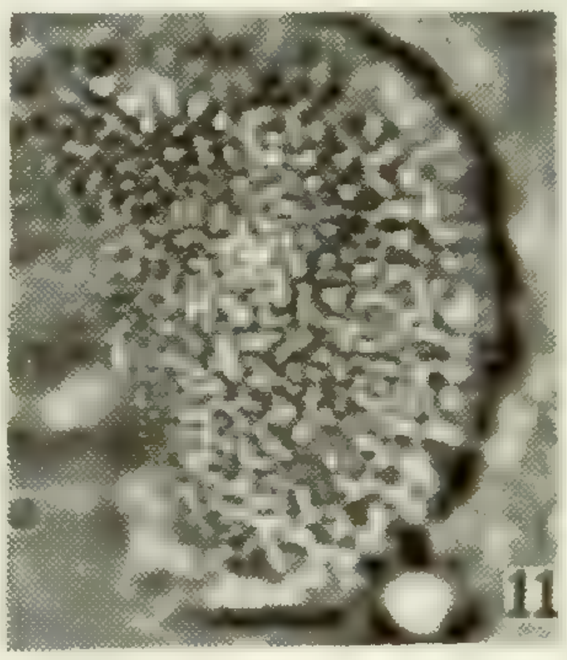












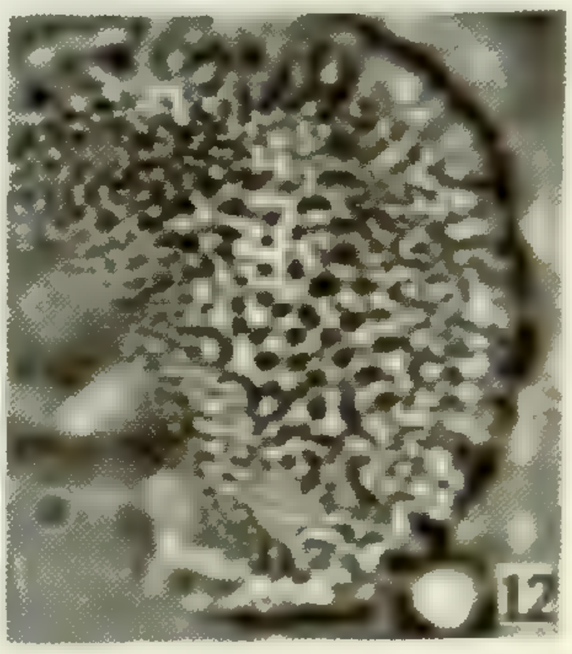
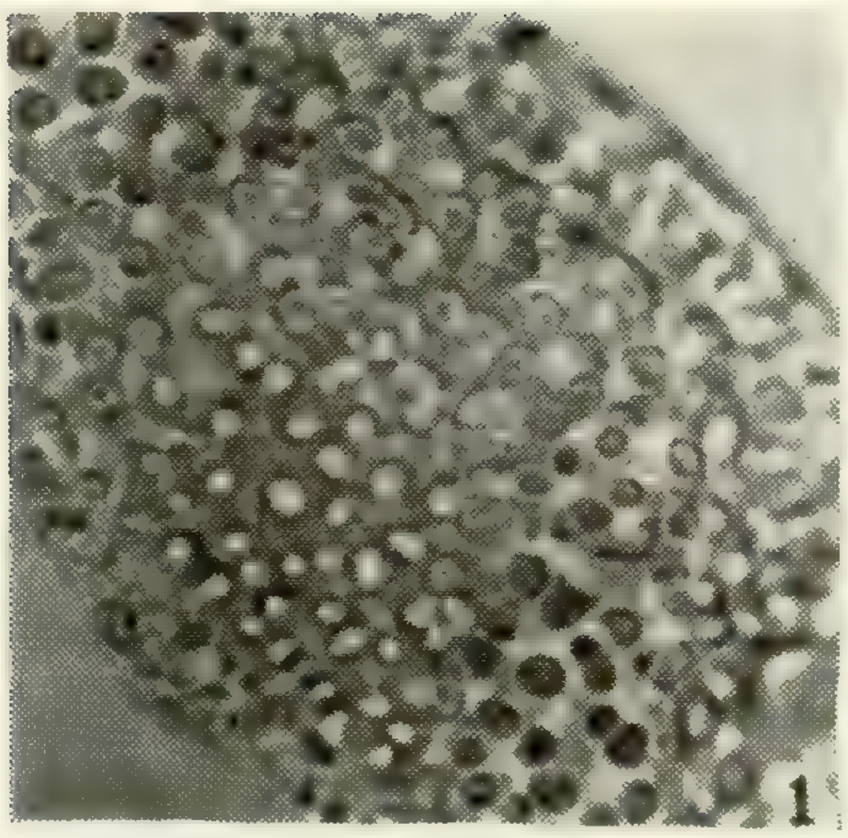
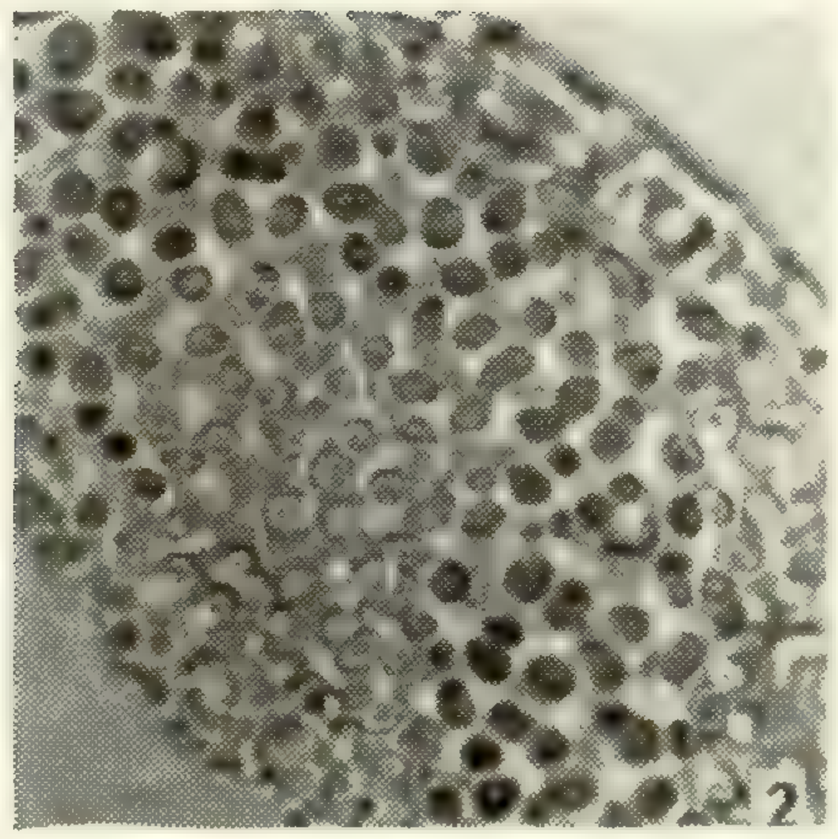
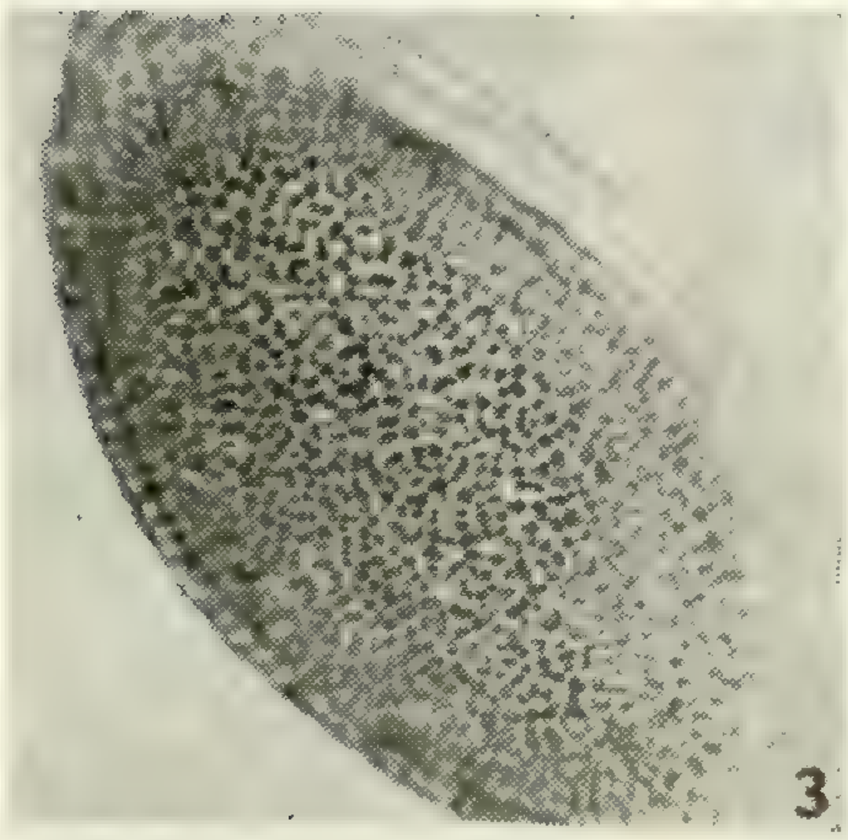


PLATE 33. FIG. 1–3. *Asimina triloba* (L.) Dunal; Fig. 1, × 200; Fig. 2,3, × 1000. FIG. 4. *A. parviflora* (Michx.) Dunal, × 200. FIG. 5. *Annona muricata* L., × 200. FIG. 6. *A. tomentosa* R. E. Fries, × 500. FIG. 7. *A. senegalensis* Pers., × 500. FIG. 8. *A. jamaicensis* Sprague, × 1000. FIG. 9. *A. ambotay* Aubl., × 500. FIG. 10–12. *A. haematantha* Miq., × 1000.







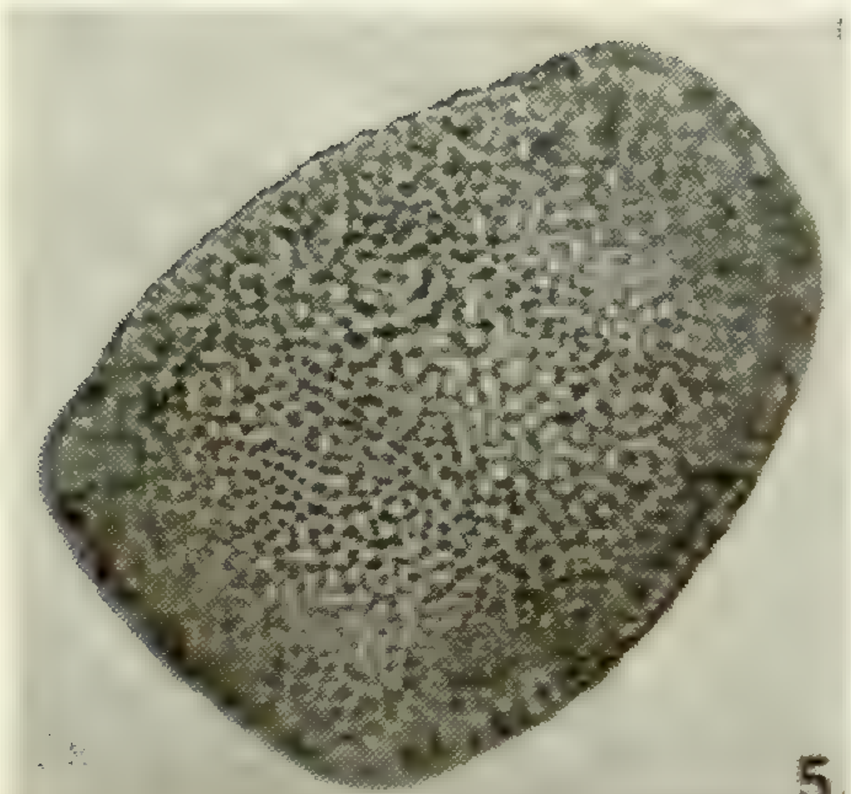
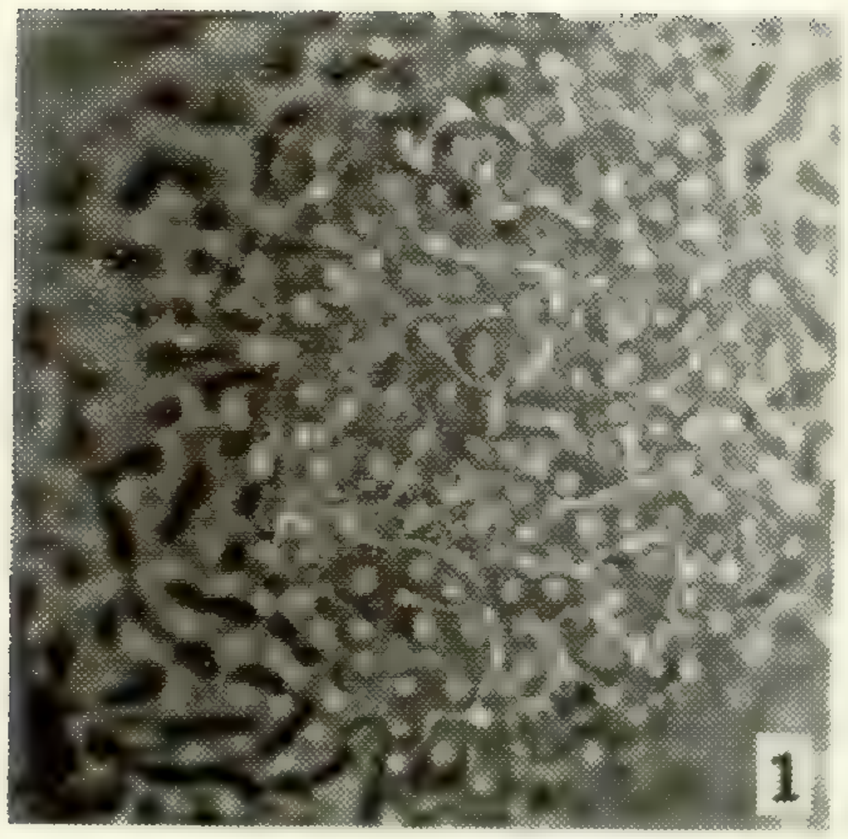
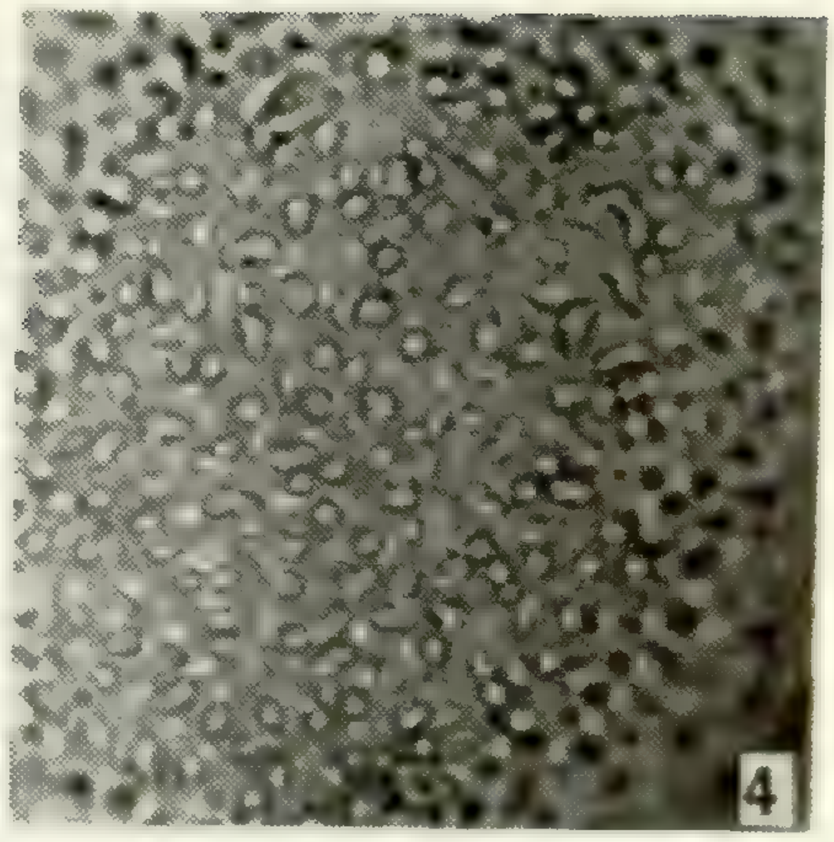
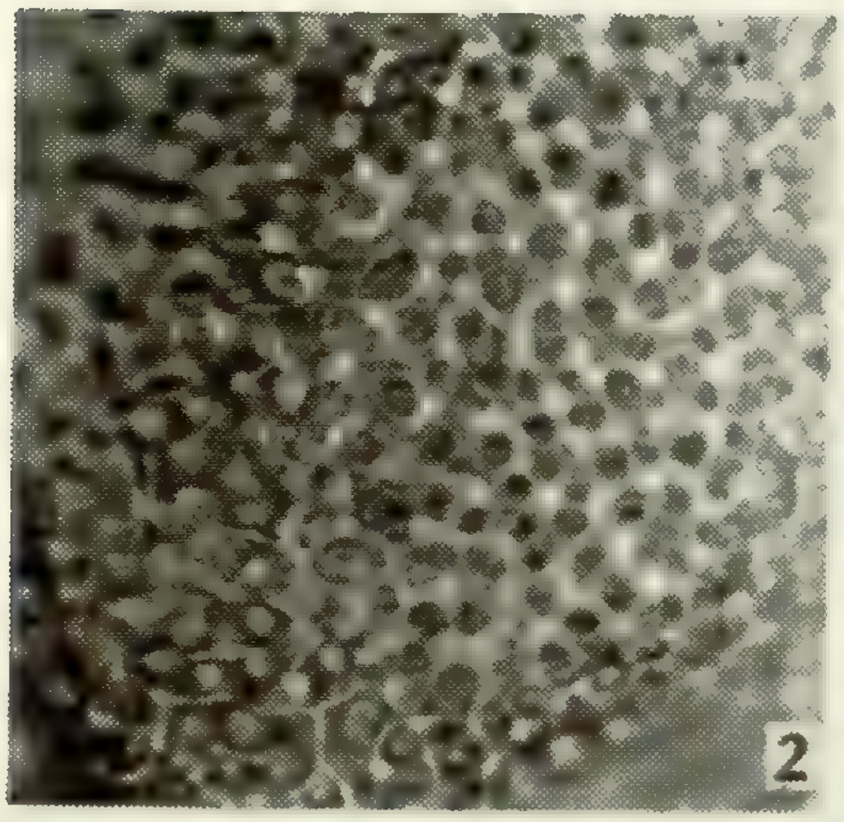
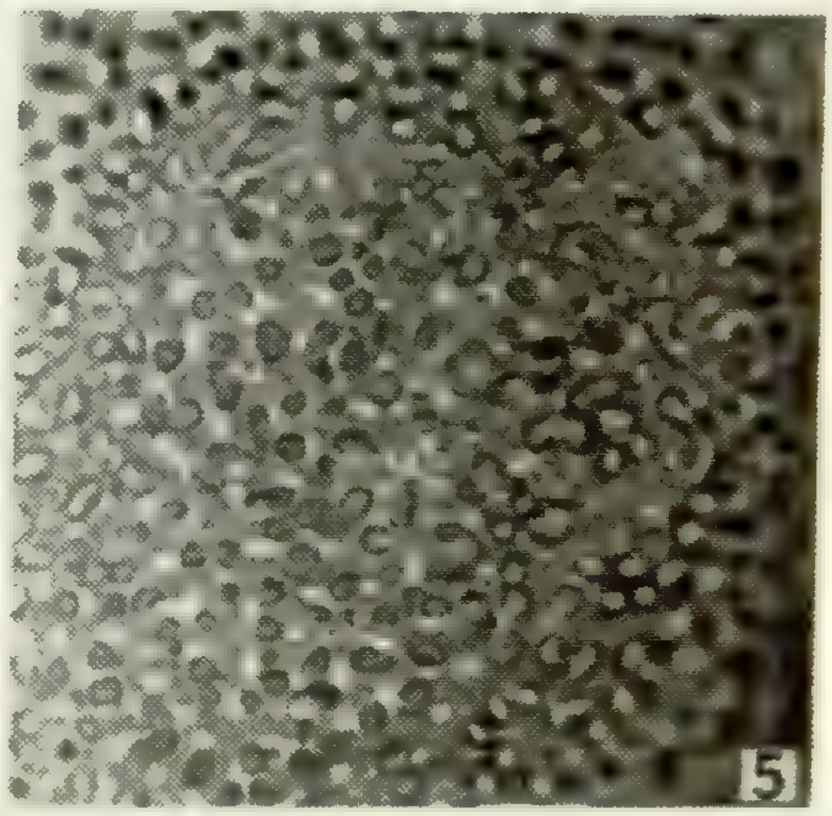


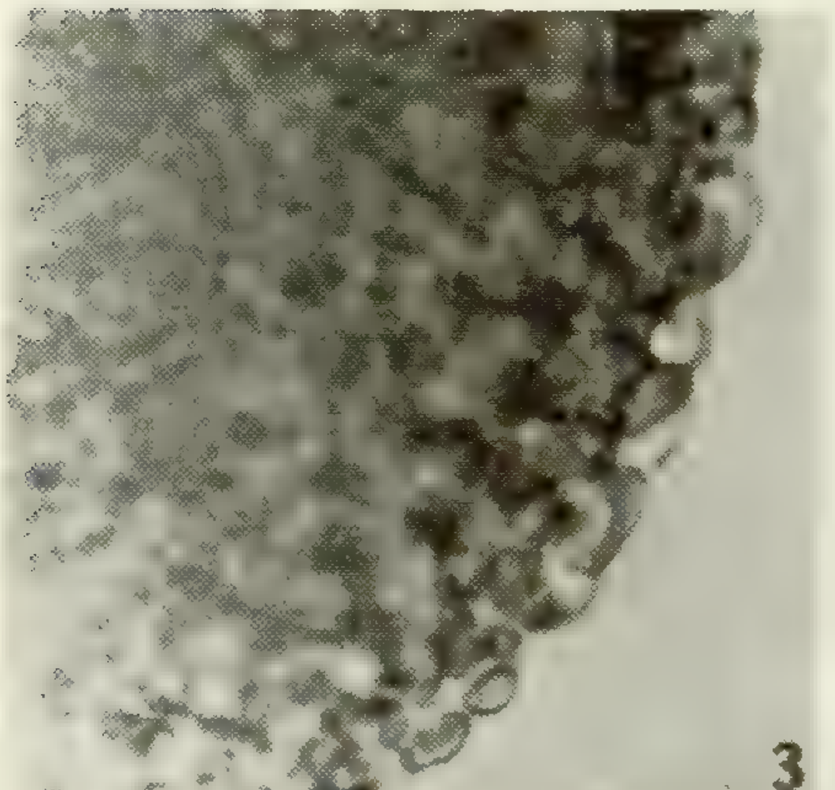
PLATE 34. FIG. 1,2. *Asimina parviflora* (Michx.) Dunal, × 1000. FIG. 3. *A. reticulata* Shuttlew. ex Chapm., × 500. FIG. 4. *A. obovata* (Willd.) Nash, × 200. FIG. 5. *A. speciosa* Nash, × 500. FIG. 6. *A. tetramera* Small, × 500.











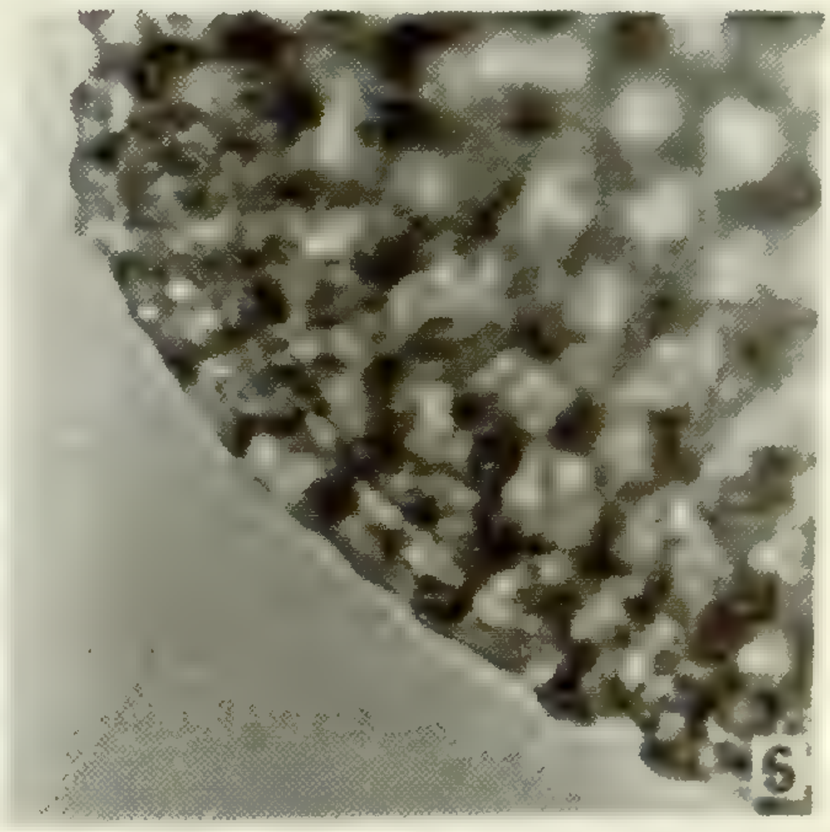
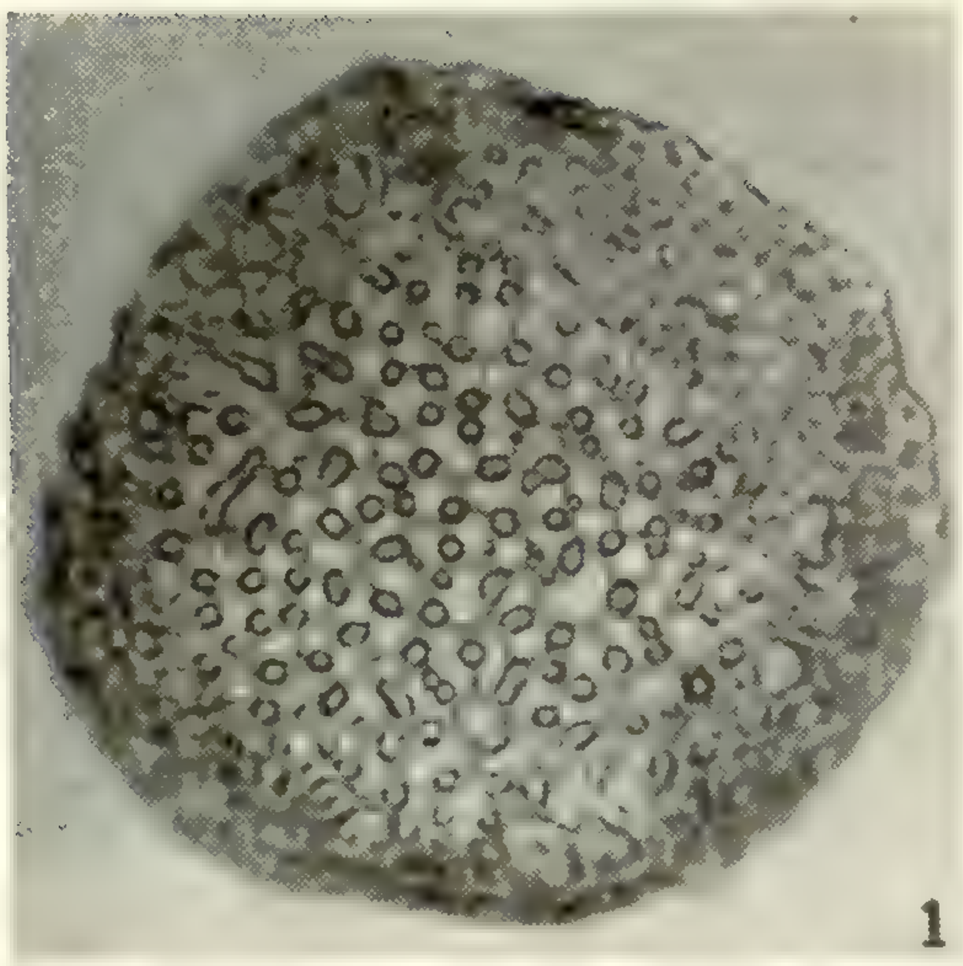


PLATE 35. FIG. 1–3. *Asimina obovata* (Willd.) Nash, × 1000. FIG. 4,5. *A. tetramera* Small, × 1000. FIG. 6. *Deeringothamnus rugelii* (Robinson) Small, × 1000.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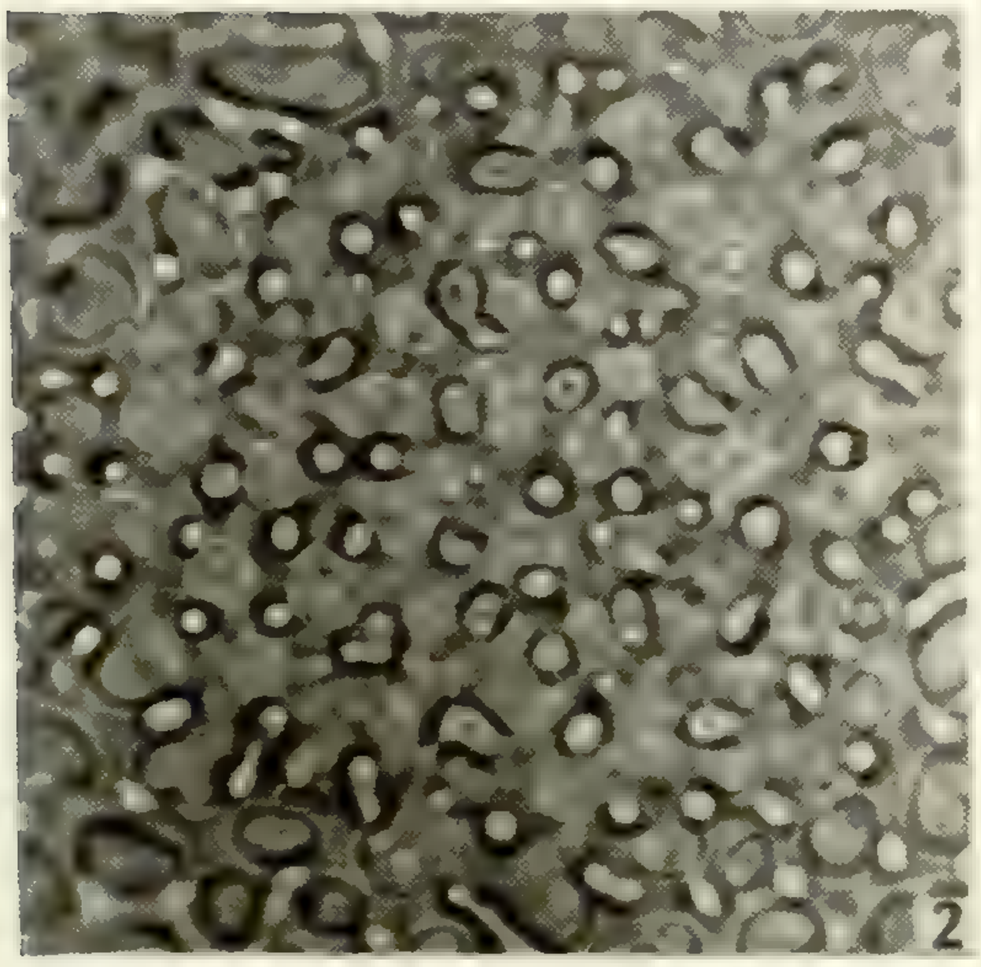
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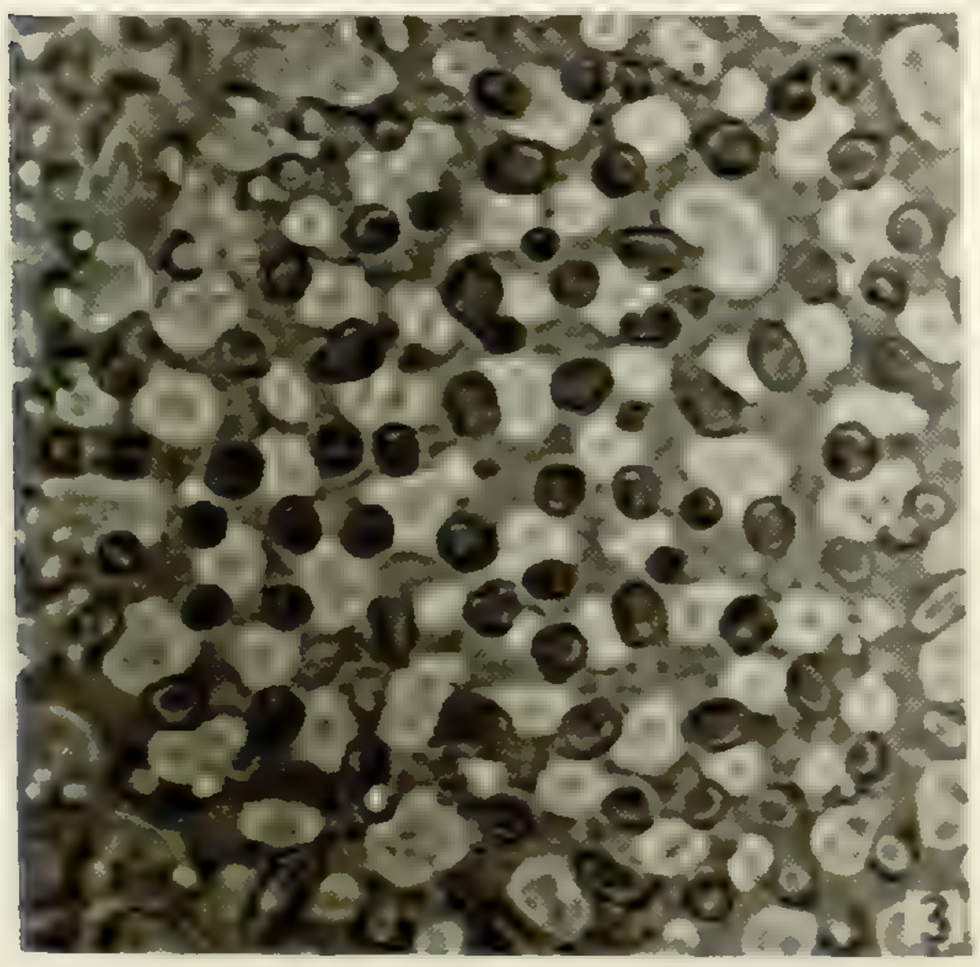
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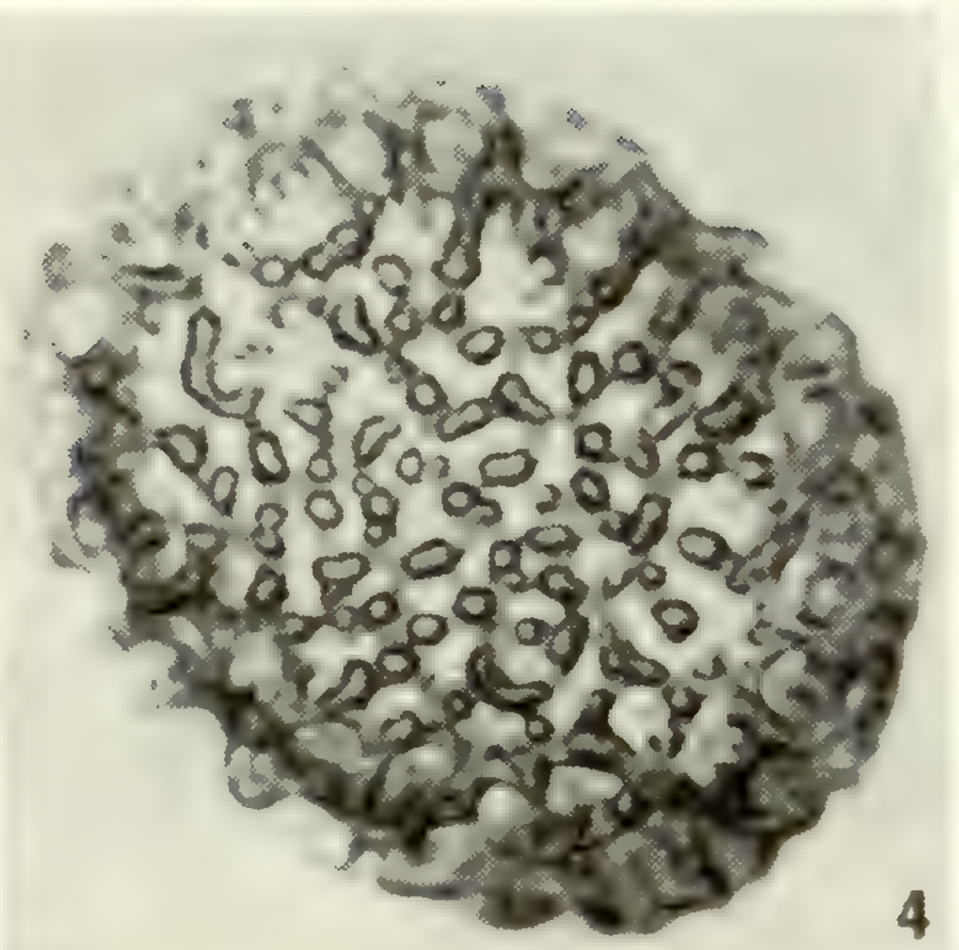
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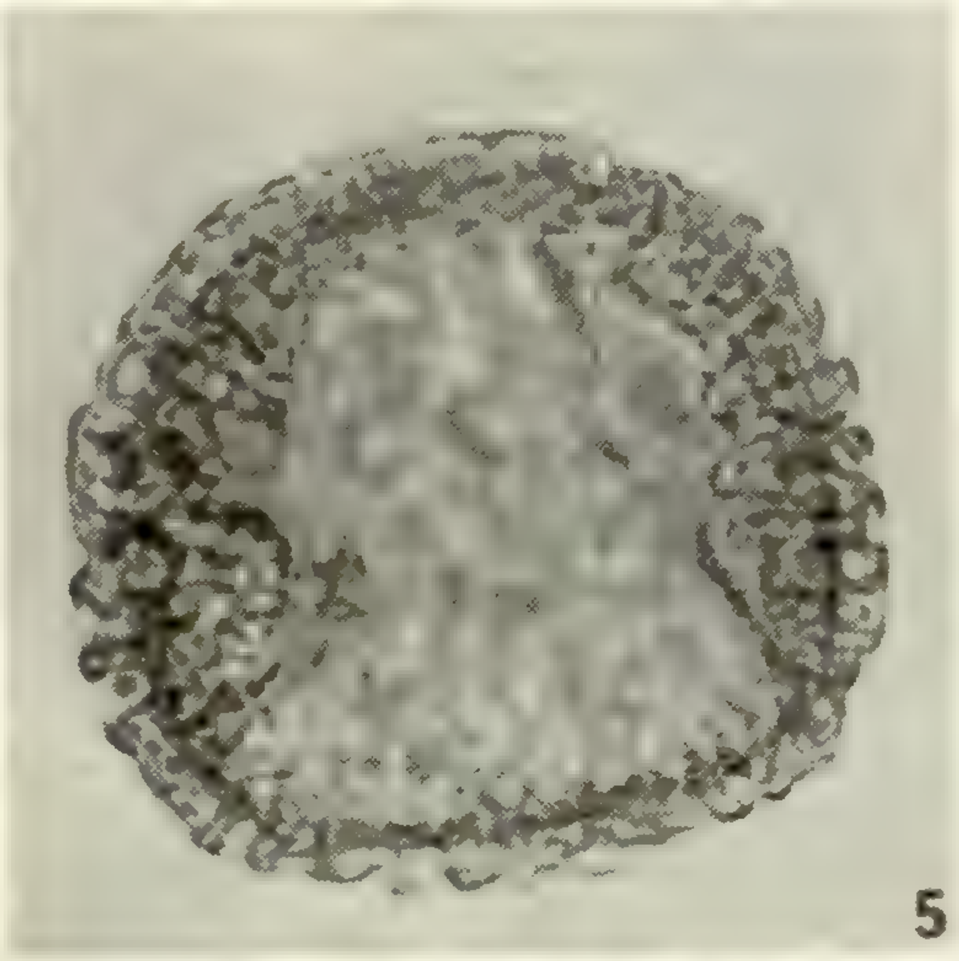
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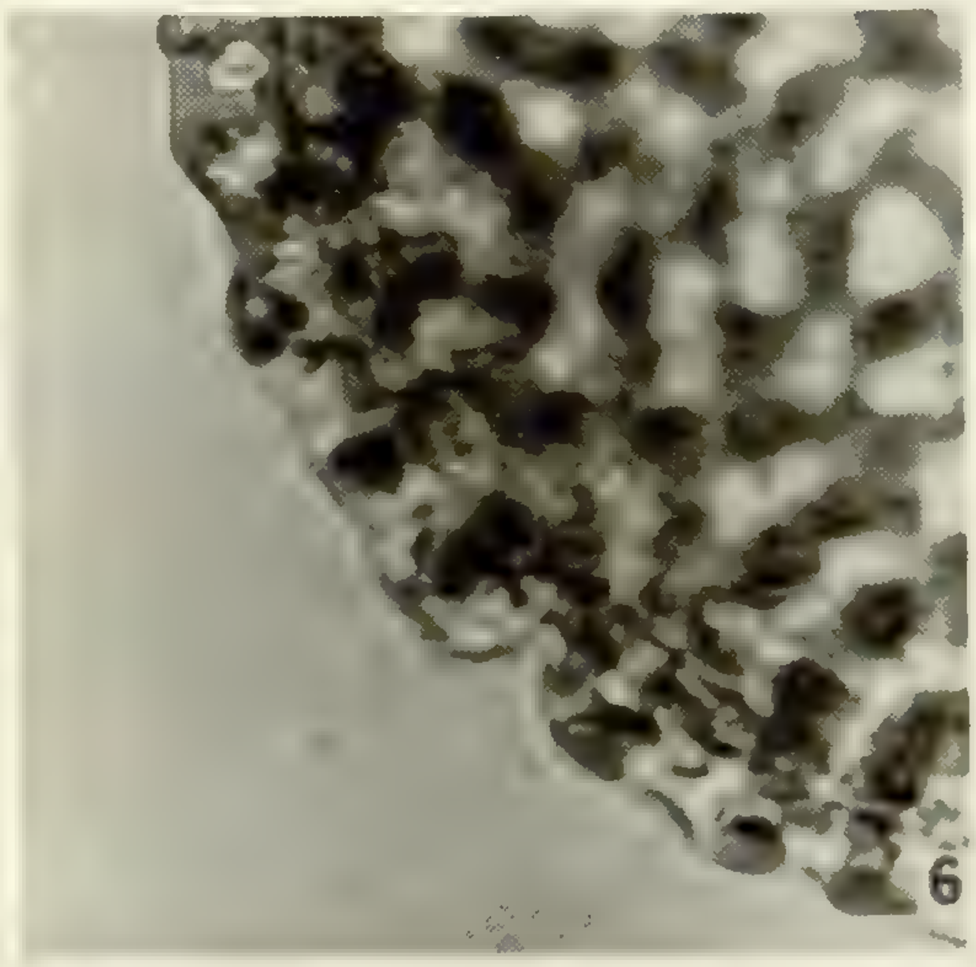
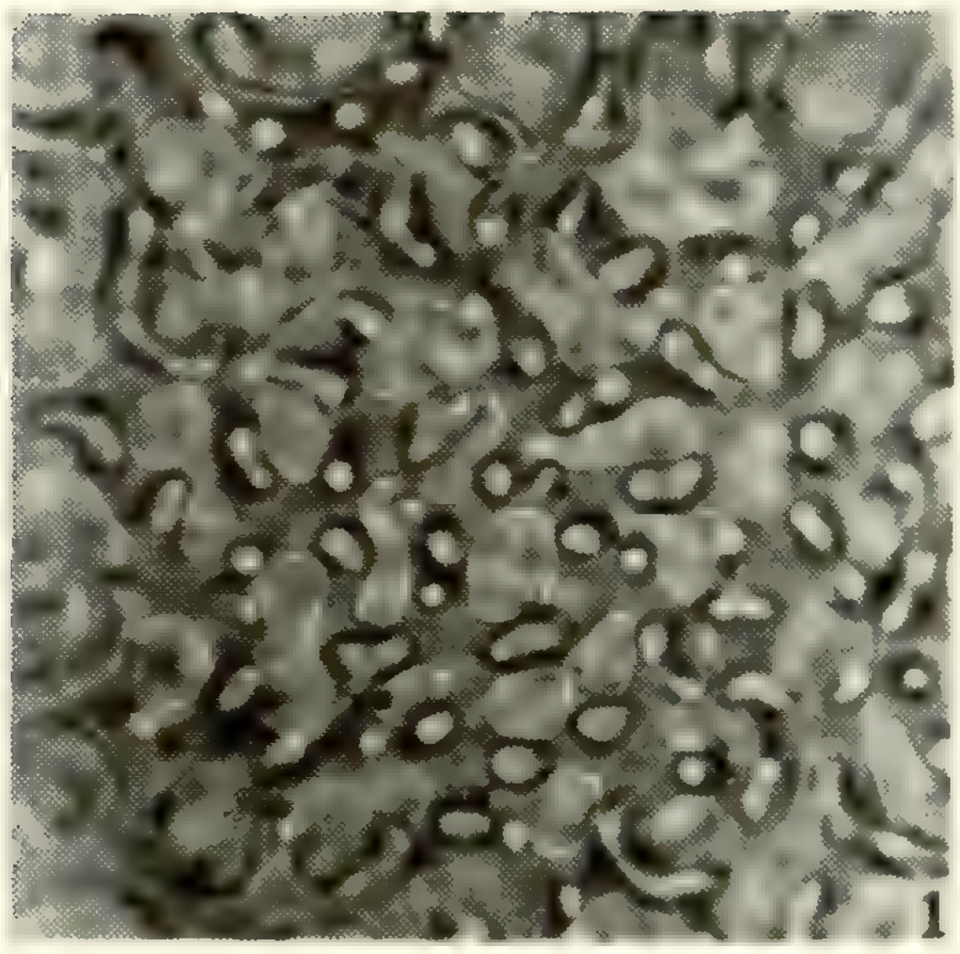
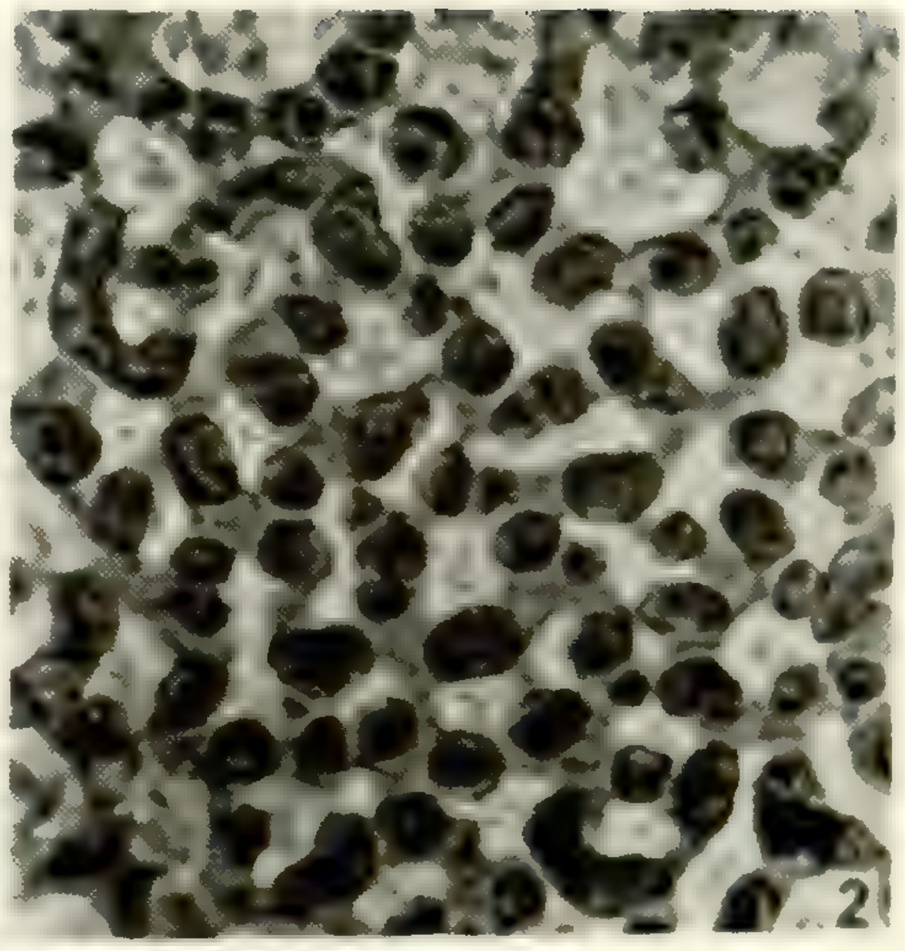
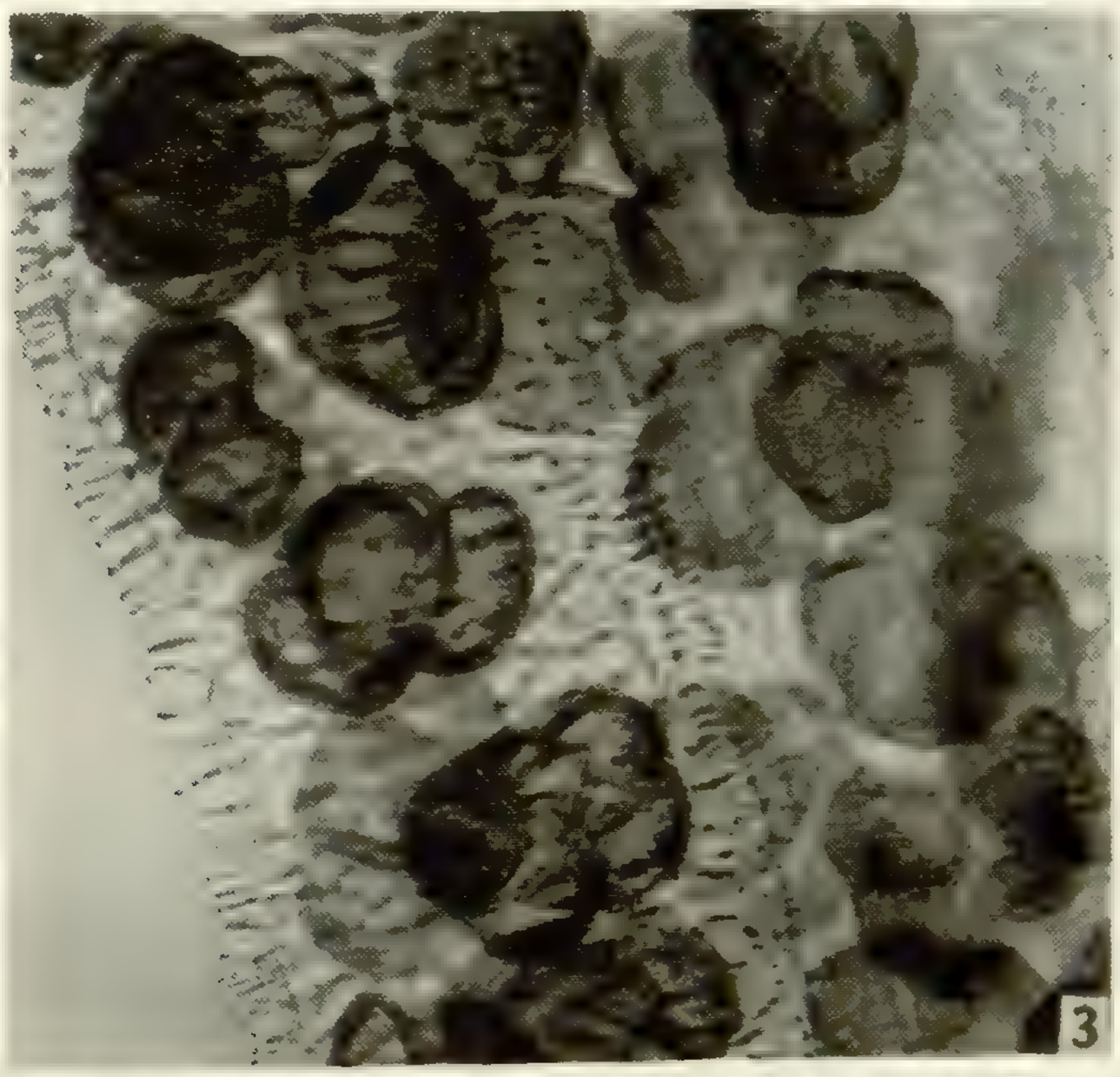
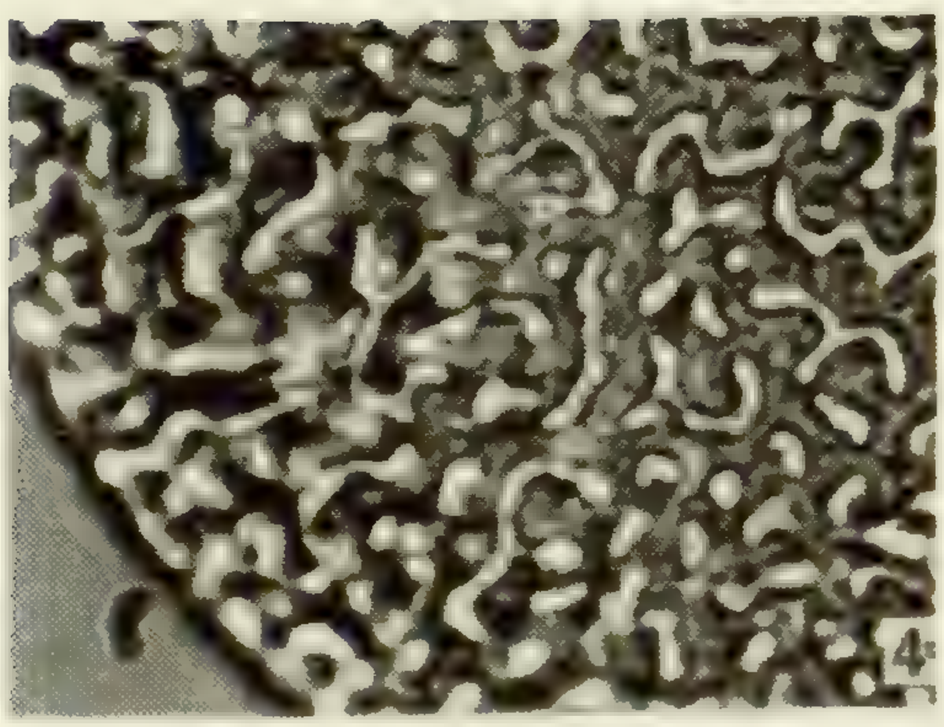

6

PLATE 36. FIG. 1–3. *Deeringothamnus rugelii* (Robinson) Small; Fig. 1, × 500; Fig. 2,3, × 1000. FIG. 4–6. *D. pulchellus* Small; Fig. 4,5, × 500; Fig. 6, × 1000.









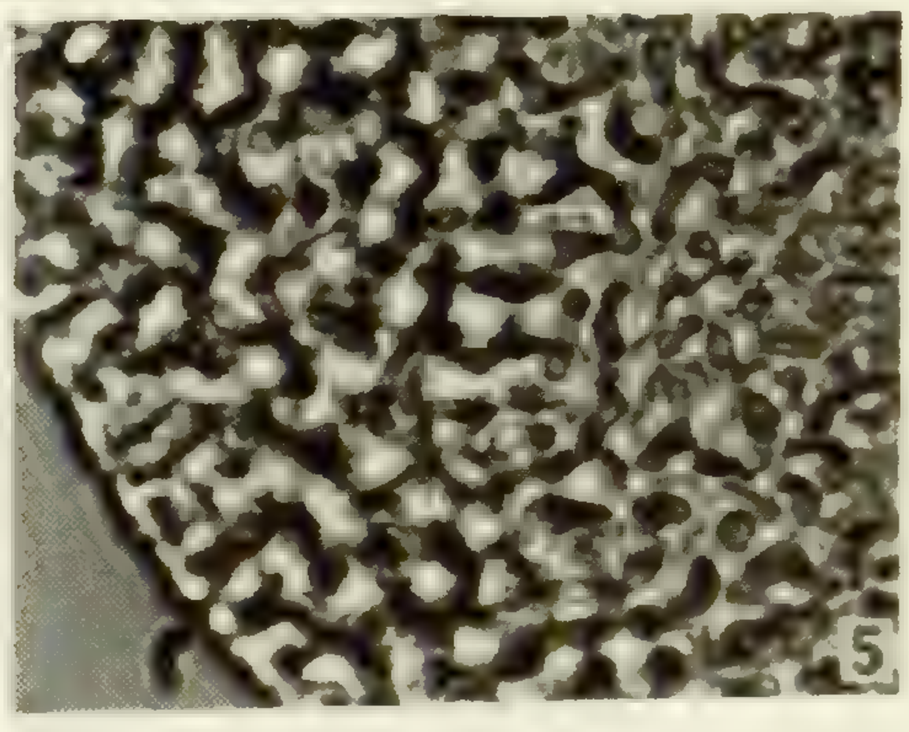
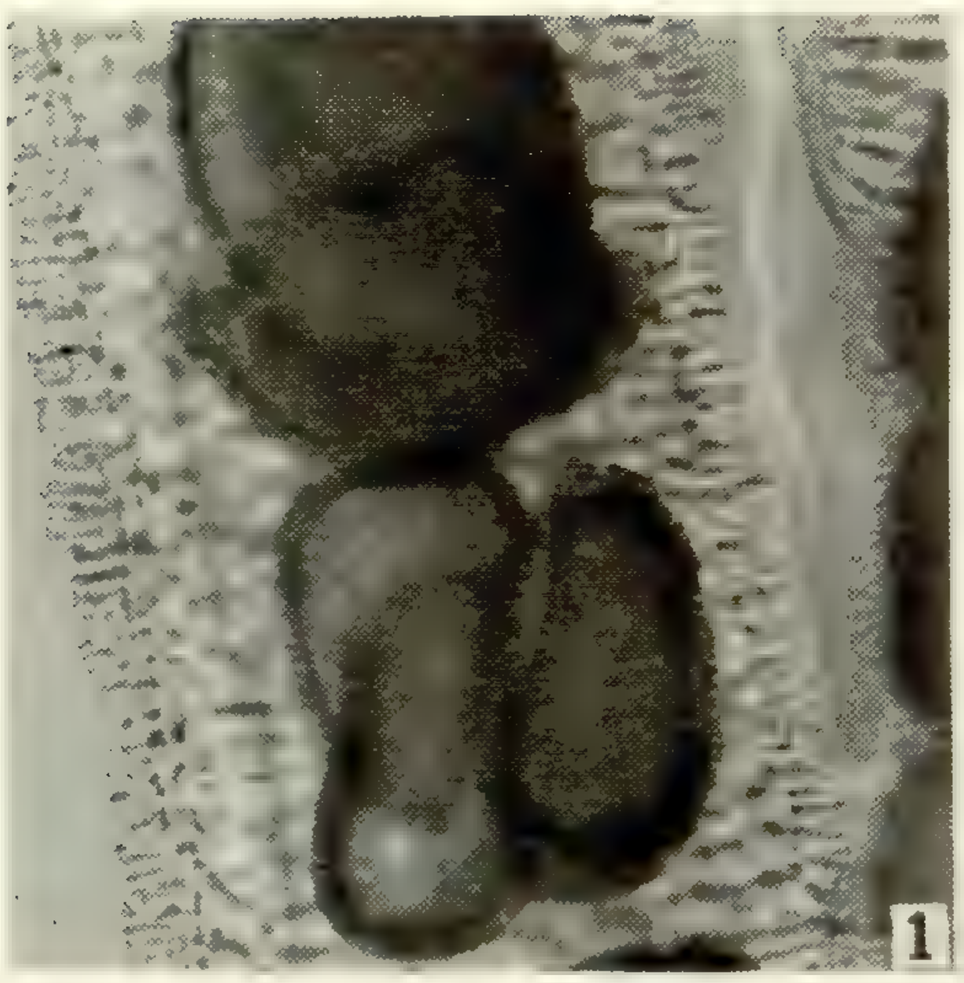
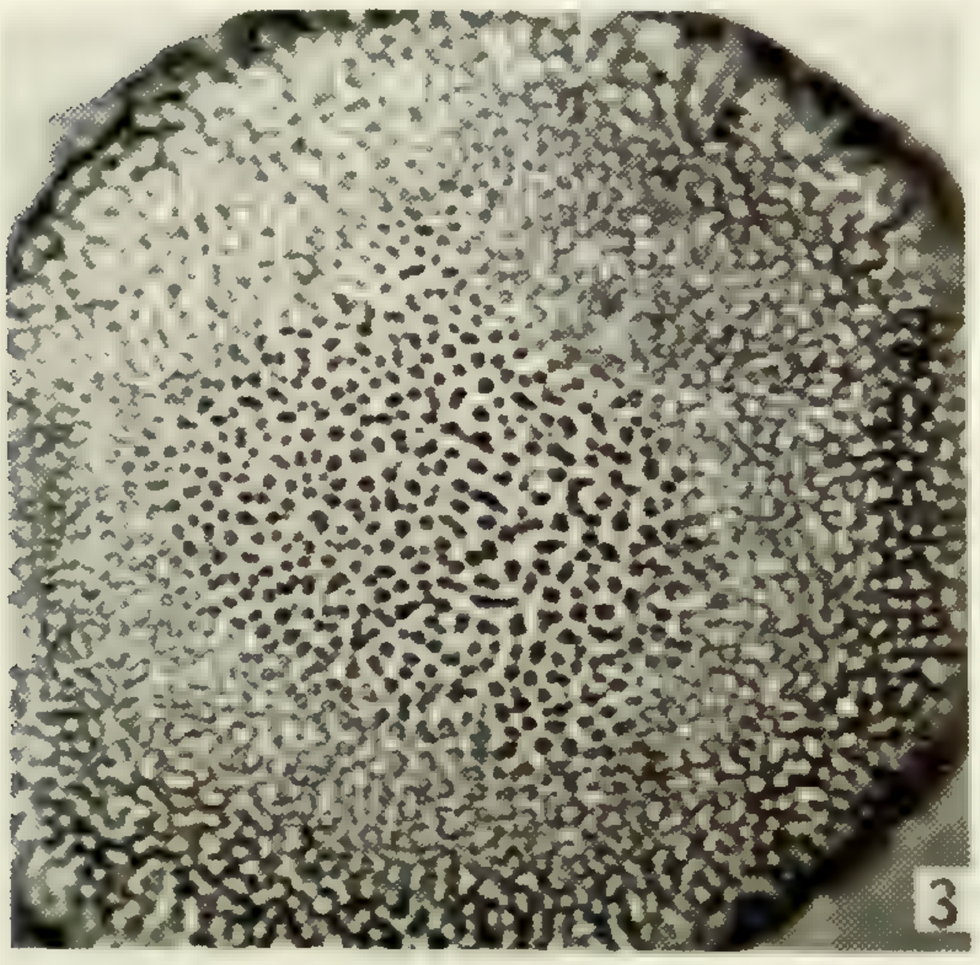


PLATE 37. FIG. 1,2. *Deeringothamnus pulchellus* Small, × 1000. FIG. 3. *Asimina pygmaea* (Bartr.) Dunal, × 200. FIG. 4,5. *Annona jahnii* Saff., × 1000.





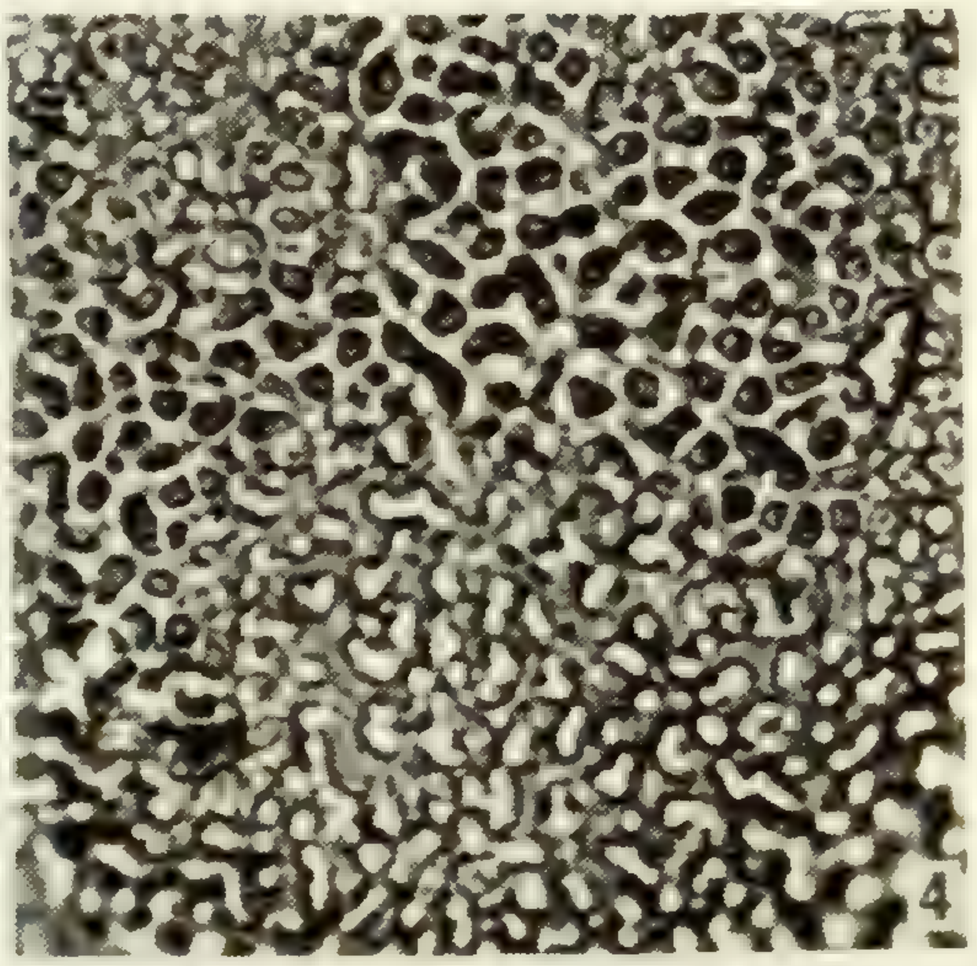
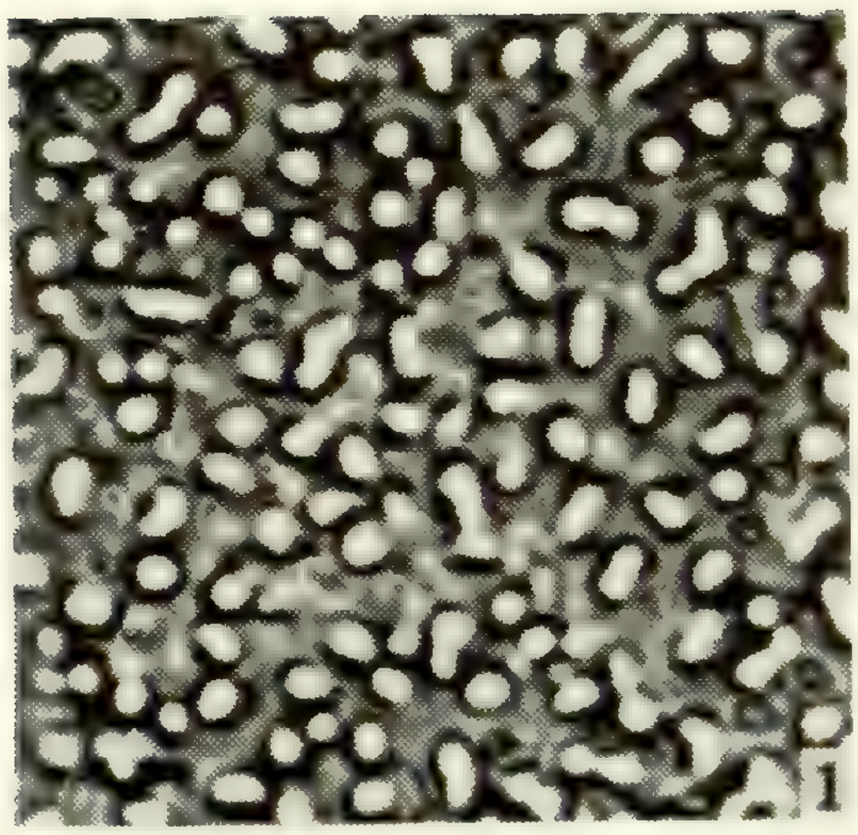
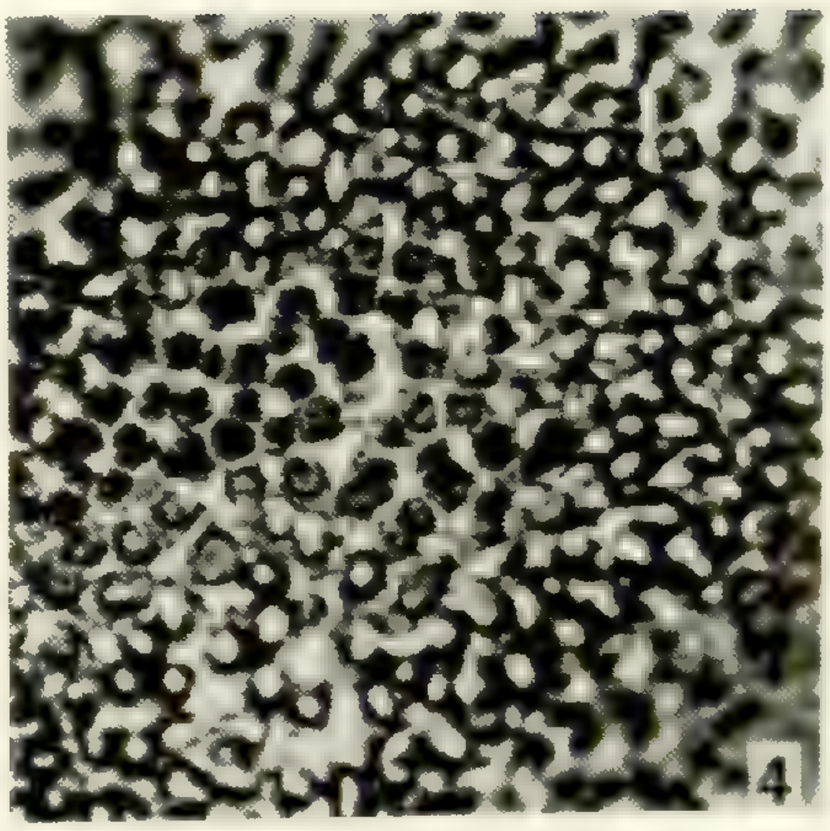
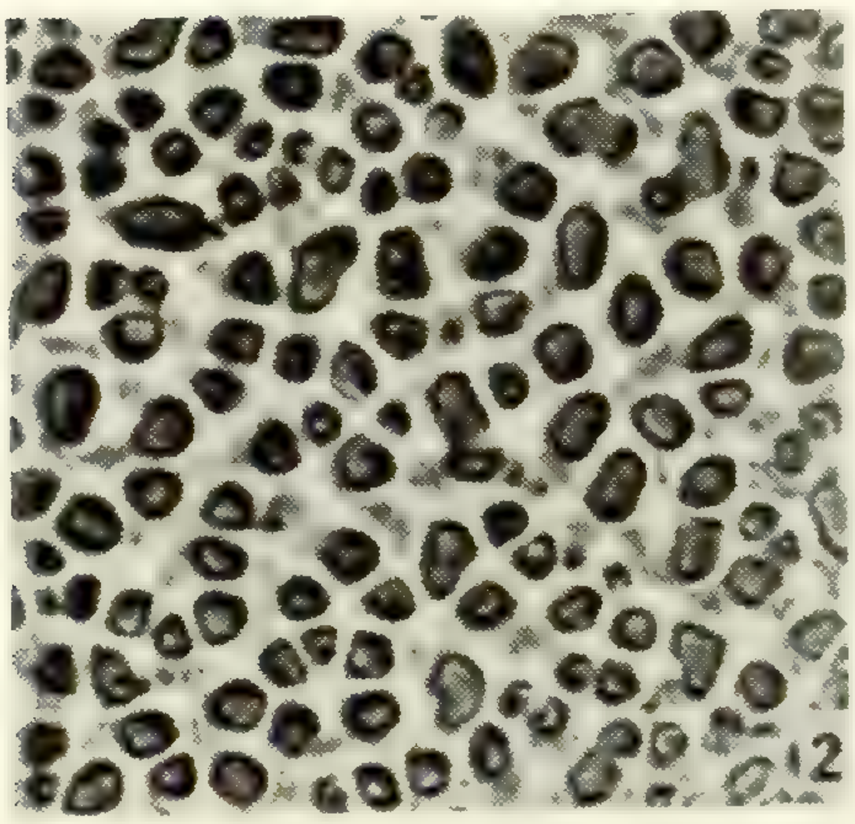
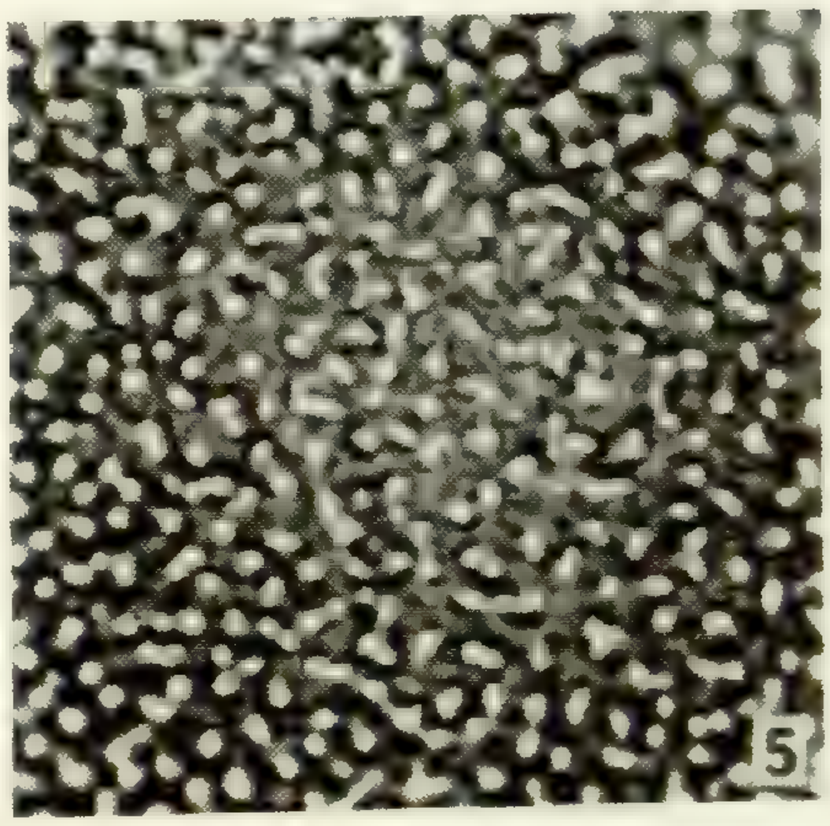


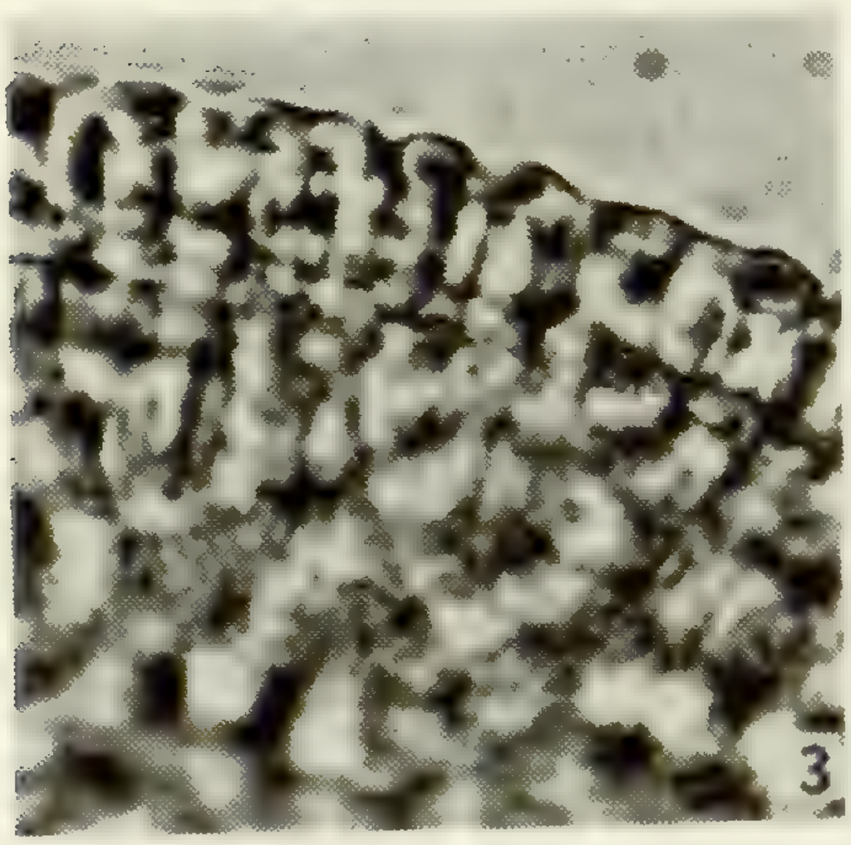
PLATE 38. FIG. 1. *Annona muricata* L., × 200. FIG. 2. *A. foetida* Mart., × 200. FIG. 3. *A. dioica* St. Hil., × 500. FIG. 4. *A. nutans* R. E. Fries, × 1000. FIG. 5. *A. longiflora* S. Wats., × 1000. FIG. 6. *A. scleroderma* Saff., × 500.











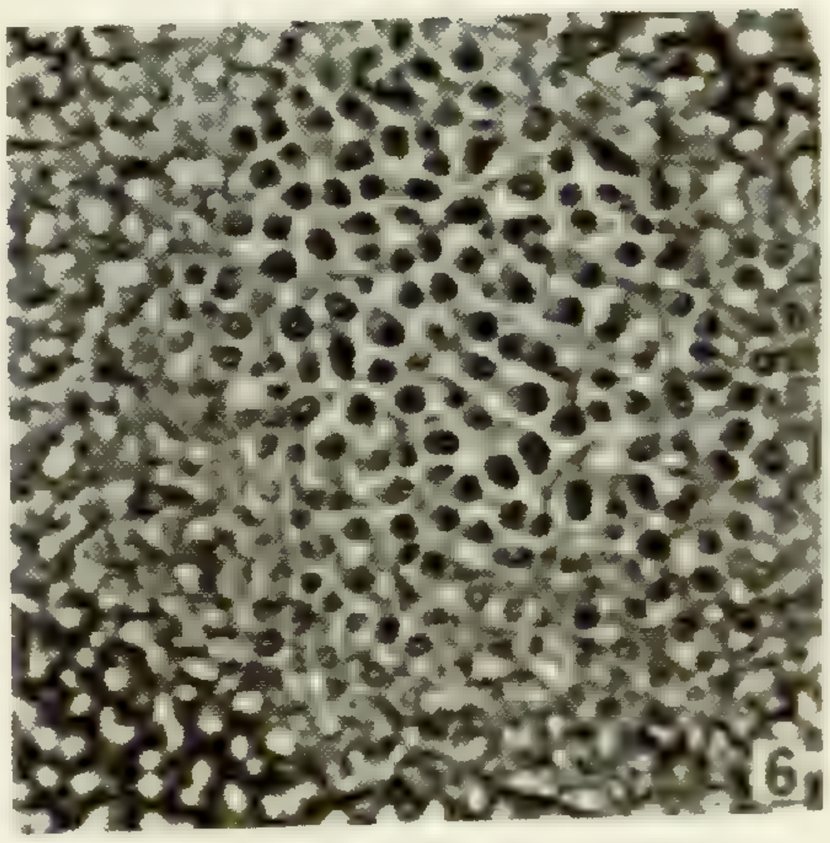
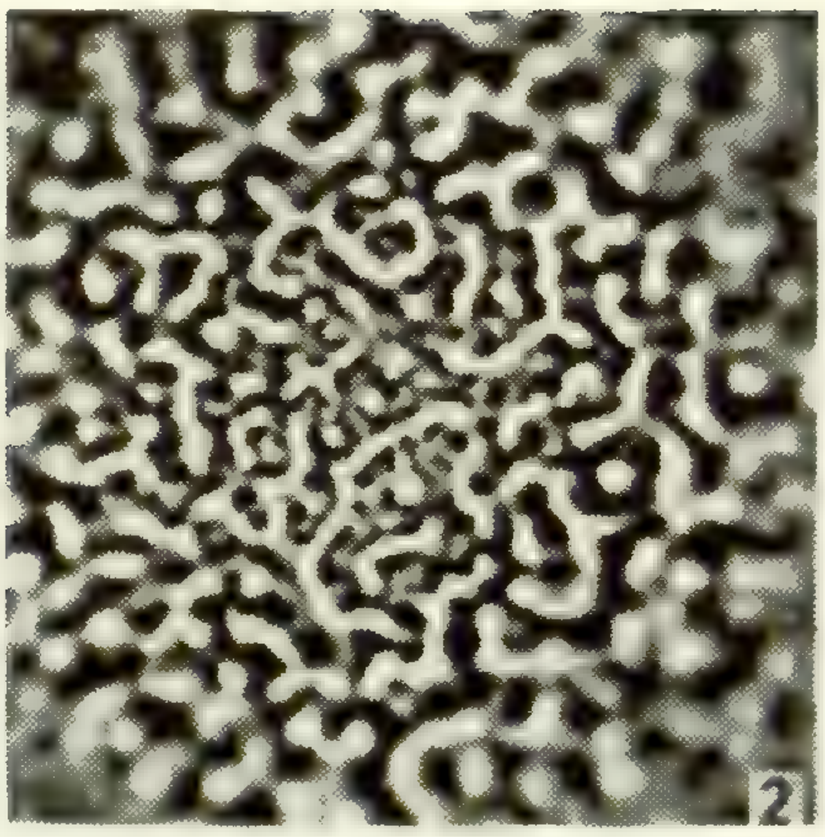
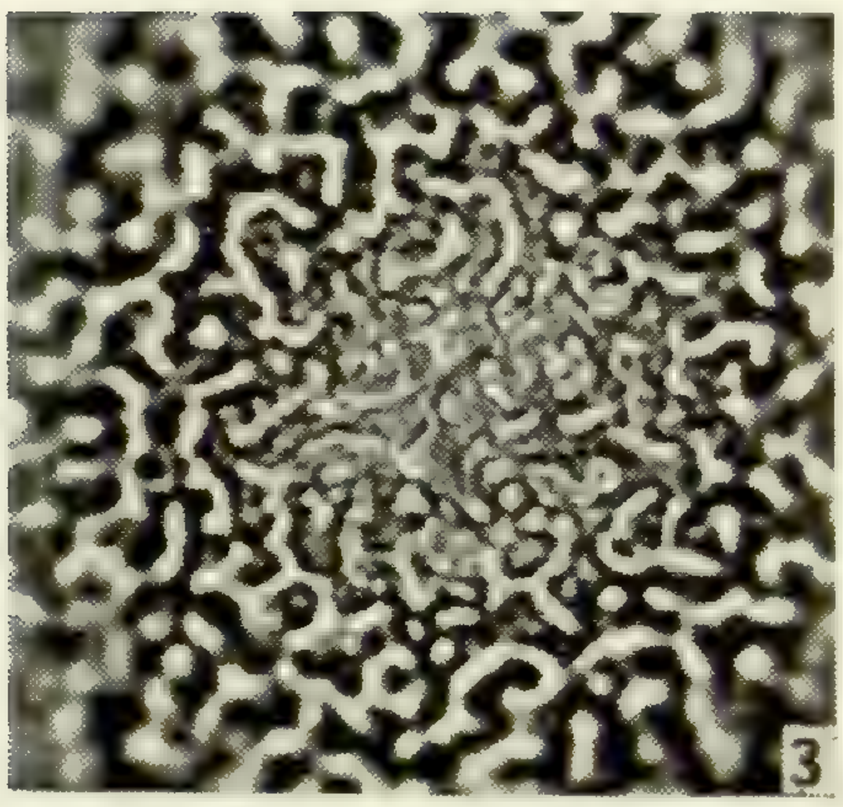
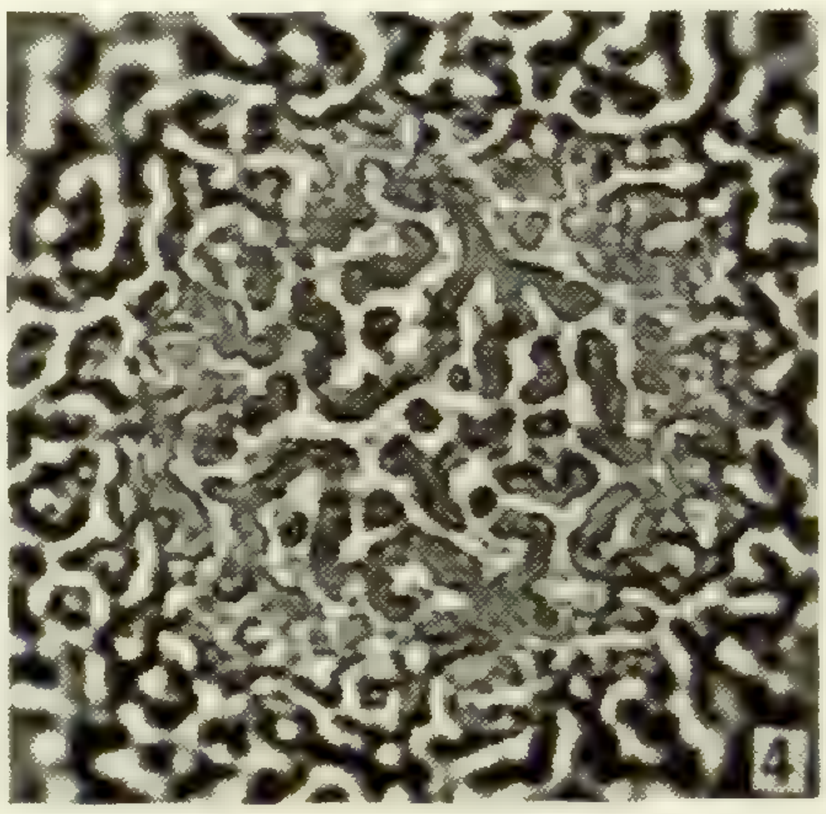
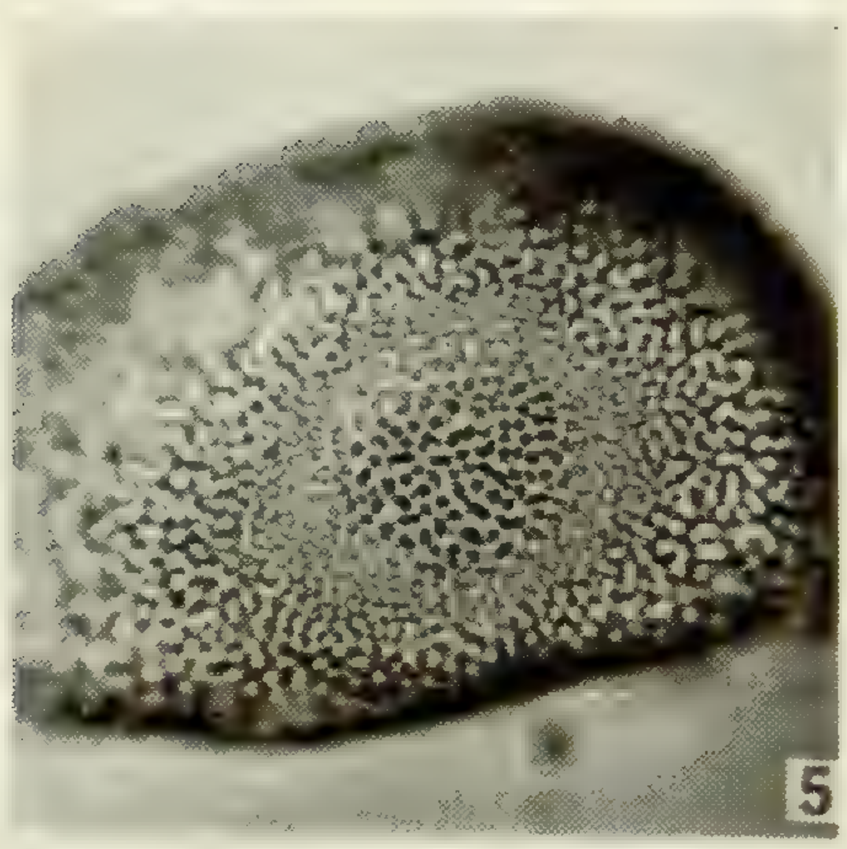


PLATE 39. FIG. 1–3. *Annona muricata* L., × 1000. FIG. 4. *A. crassiflora* Mart., × 1000. FIG. 5,6. *A. dioica* St. Hil., × 1000.









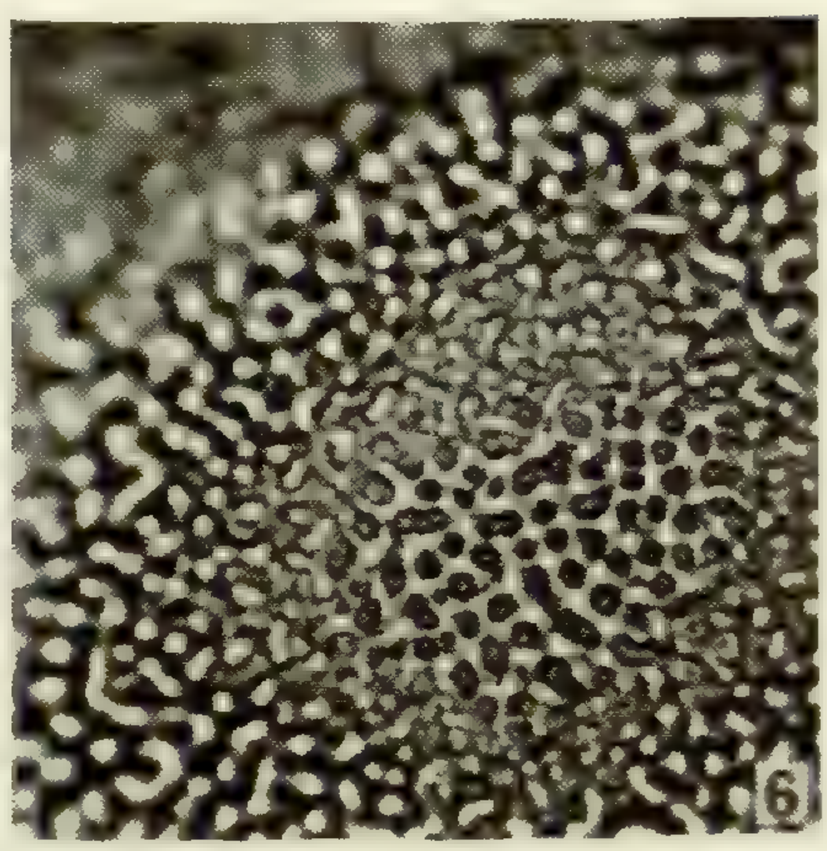
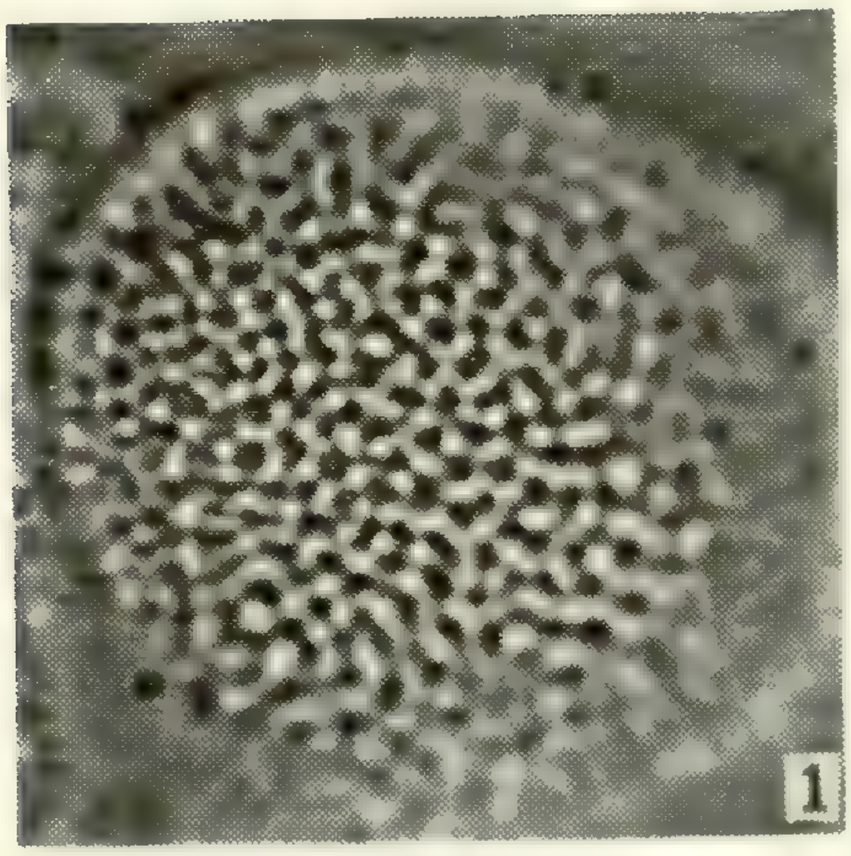
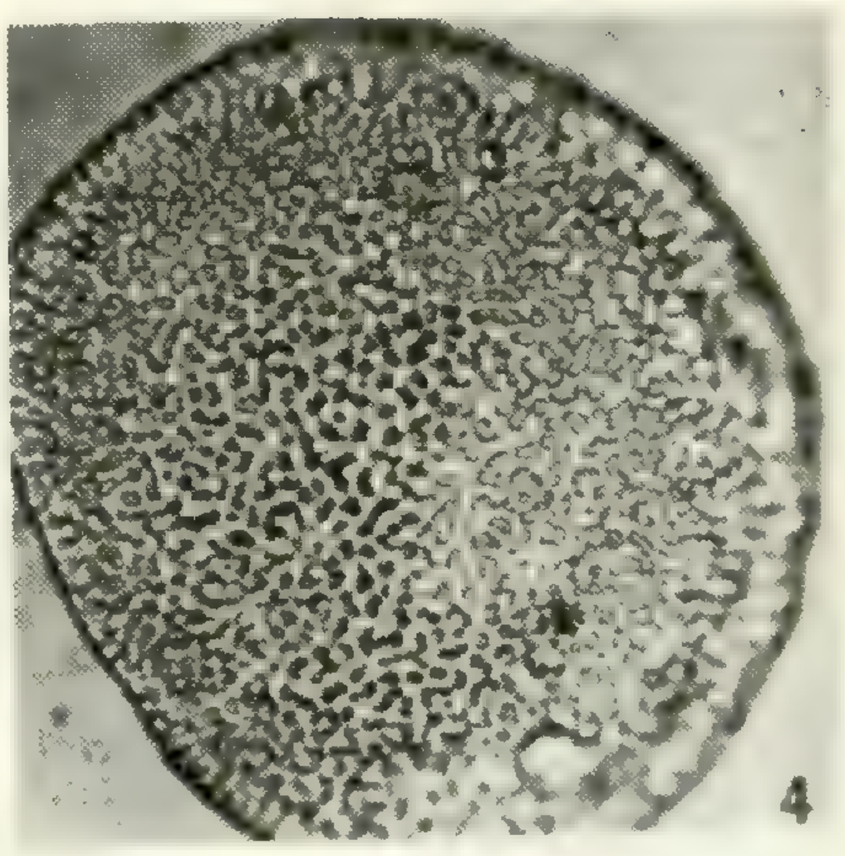
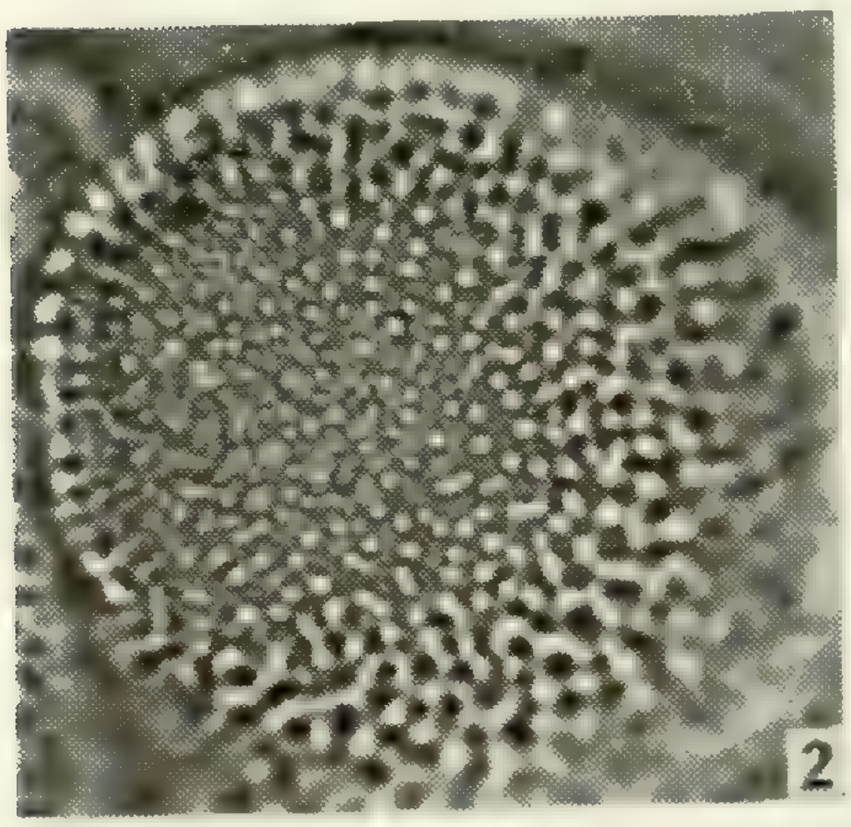
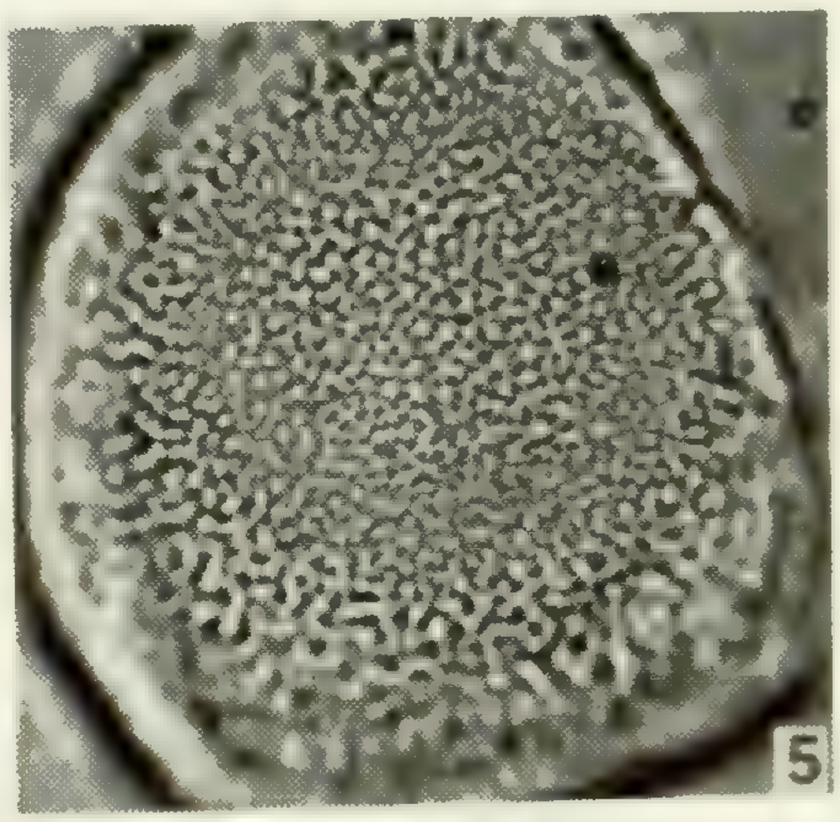


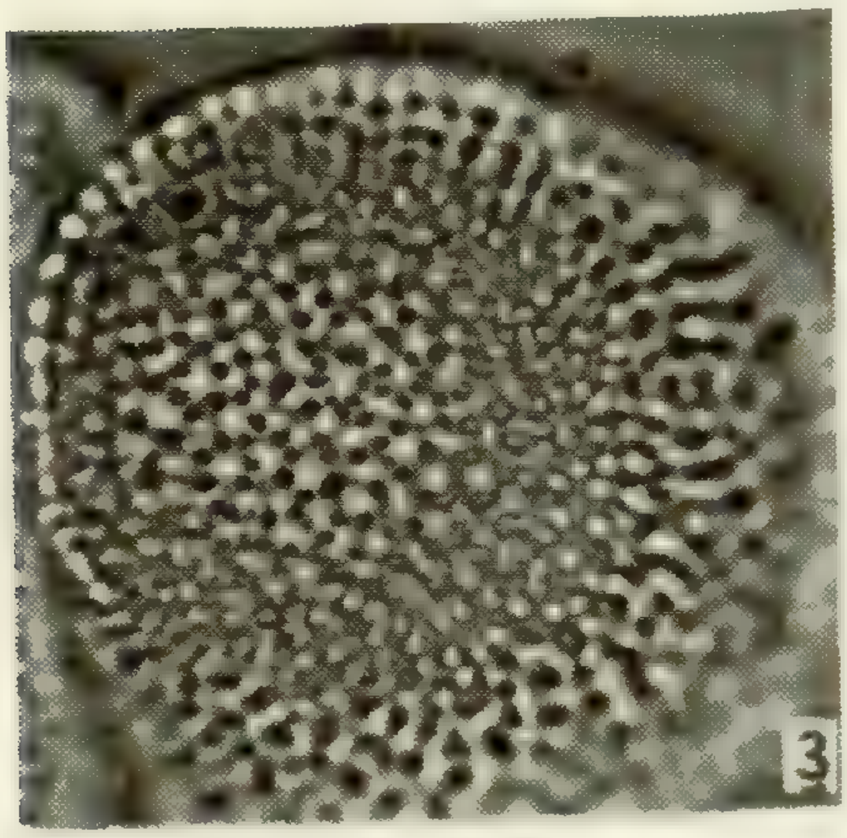
PLATE 40. FIG. 1–4. *Annona glabra* L.; Fig. 1, × 500; Fig. 2,3,4, × 1000. FIG. 5,6. *A. tessmannii* Diels; Fig. 5, × 500; Fig. 6, × 1000.











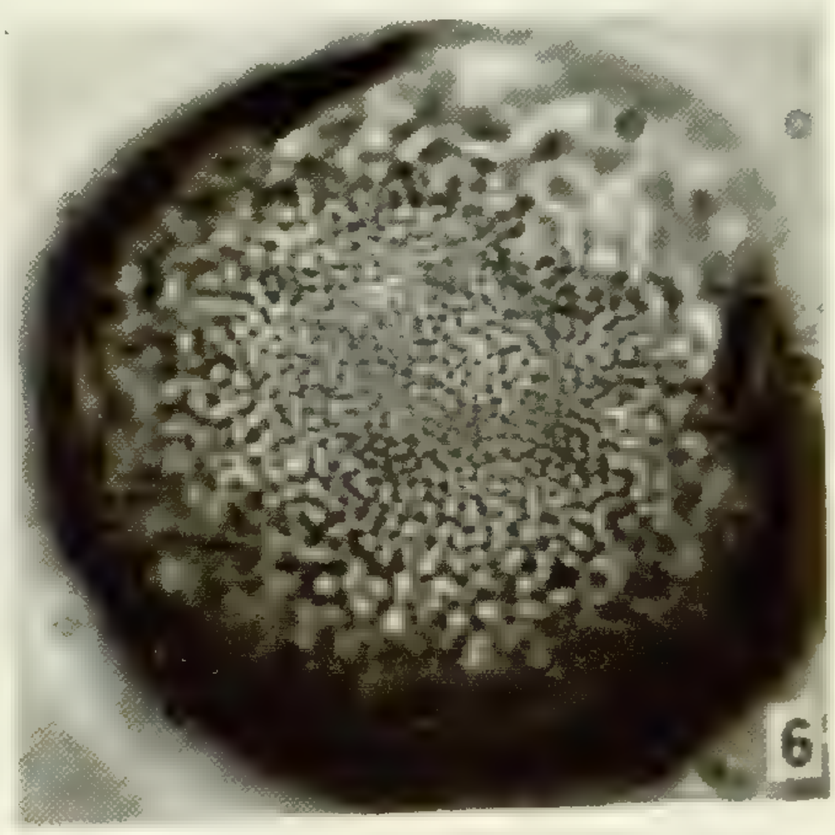
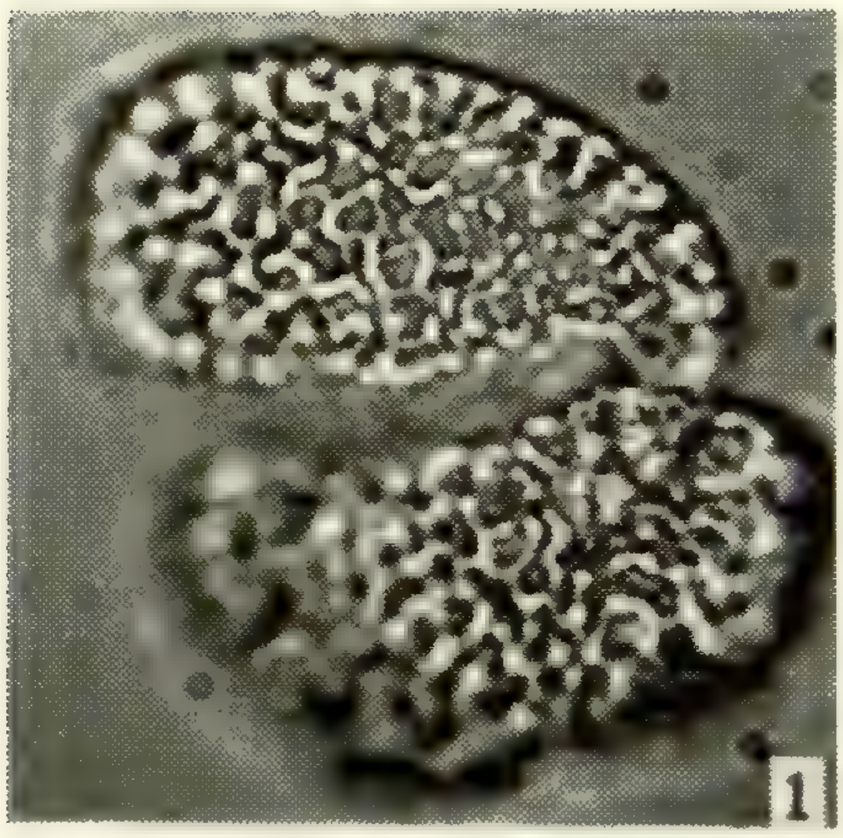
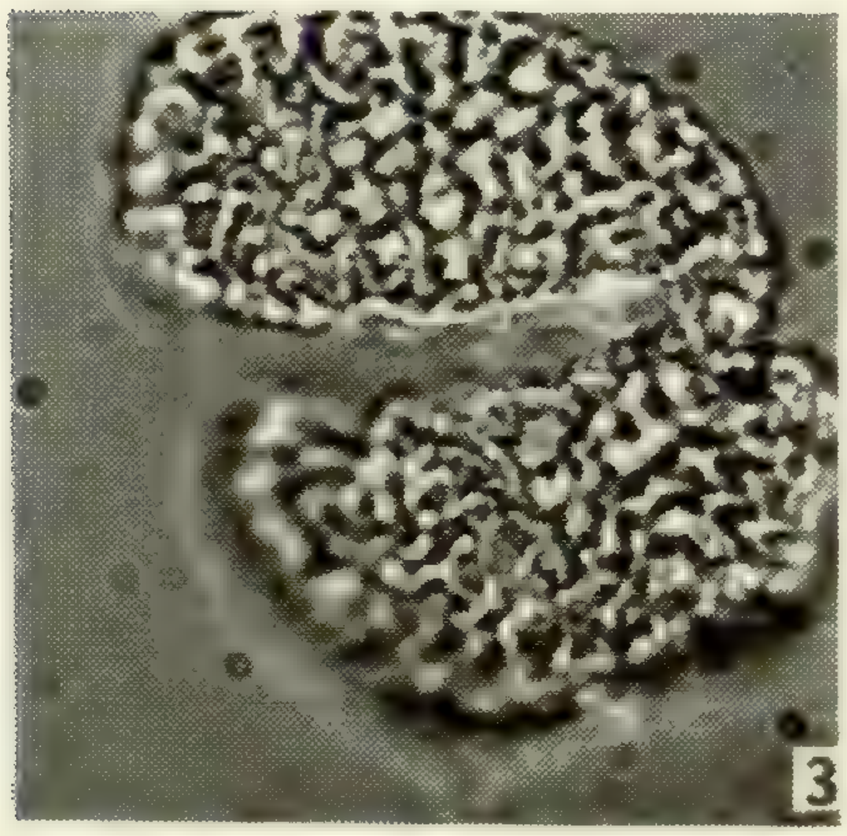
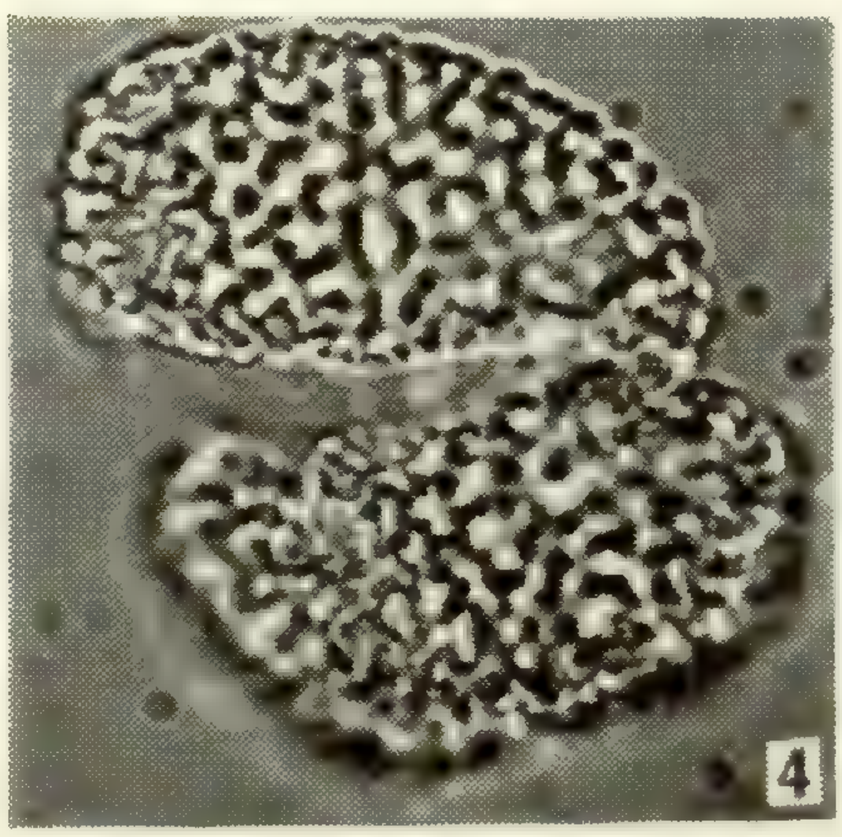


PLATE 41. FIG. 1–3. *Annona senegalensis* Pers., × 1000. FIG. 4. *A. nutans* R. E. Fries, × 500. FIG. 5. *A. acutiflora* Mart., × 1000. FIG. 6. *A. squamosa* L., × 1000.







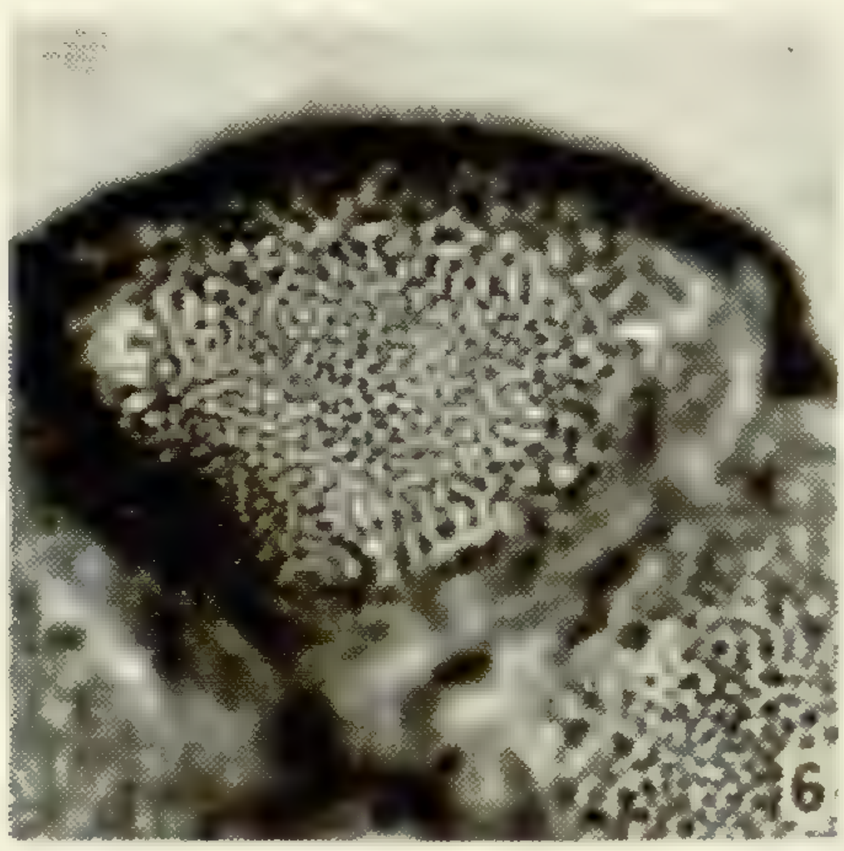
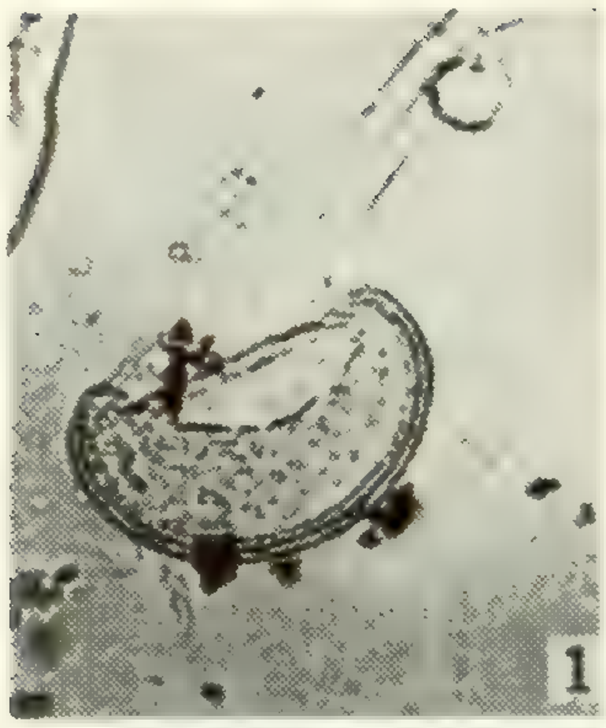
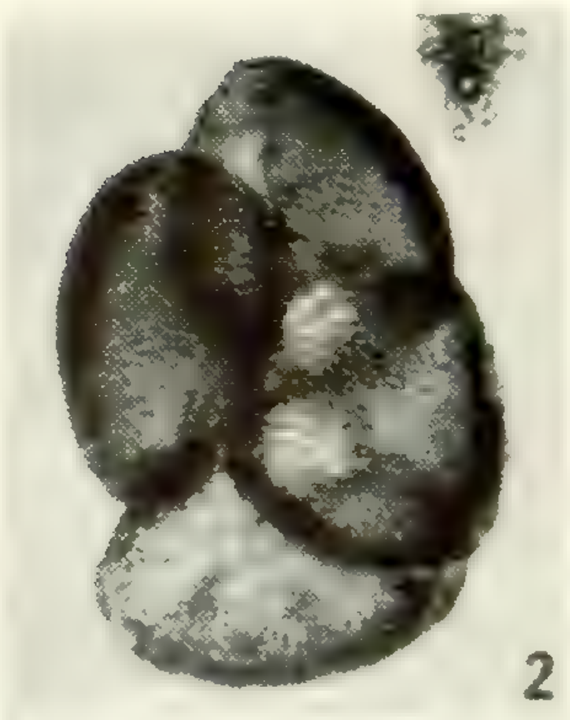
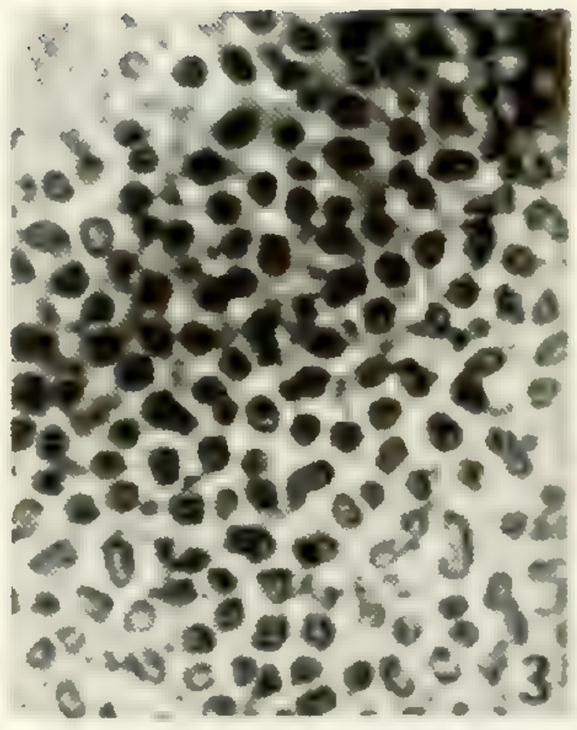
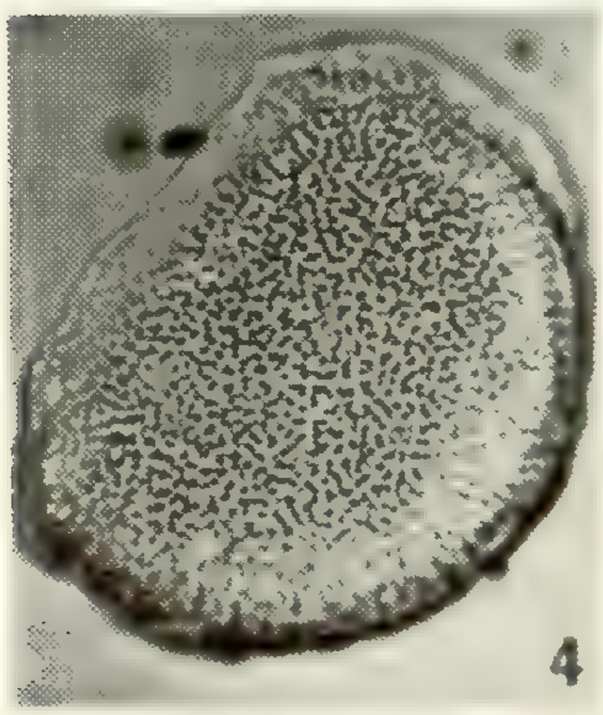


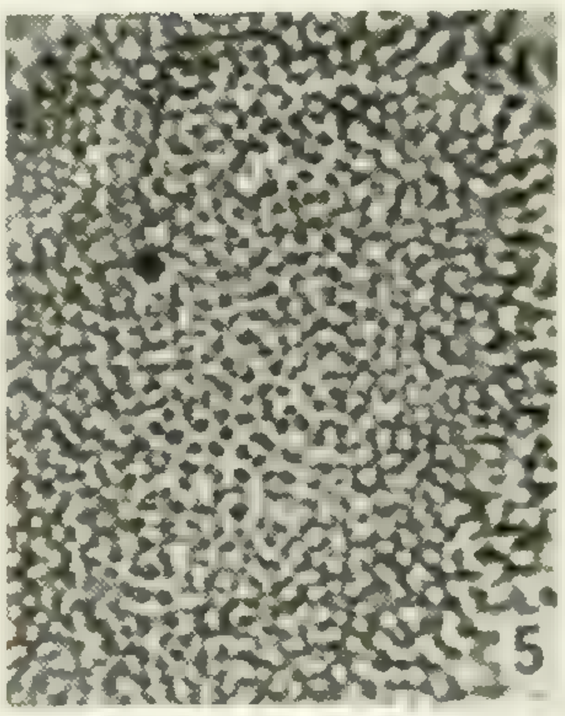
PLATE 42. FIG. 1–4. *Annona ambotay* Aubl., × 1000. FIG. 5,6. *A. reticulata* L.; Fig. 5, × 500; Fig. 6, × 1000.

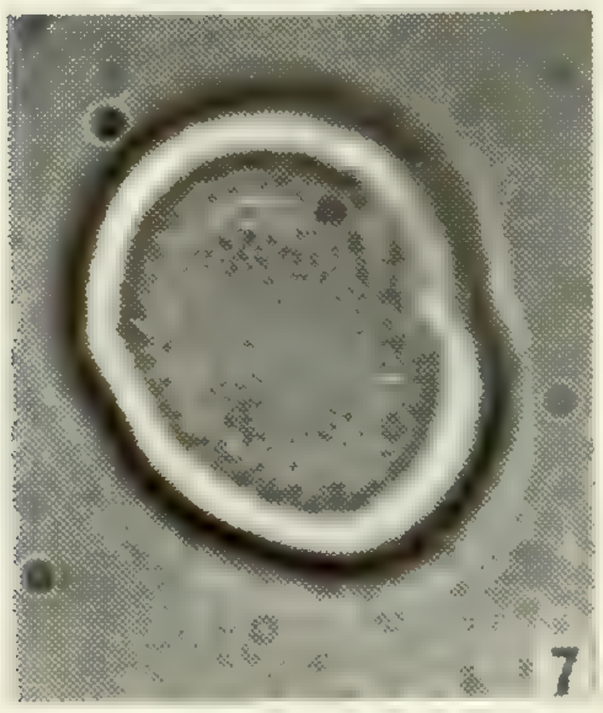


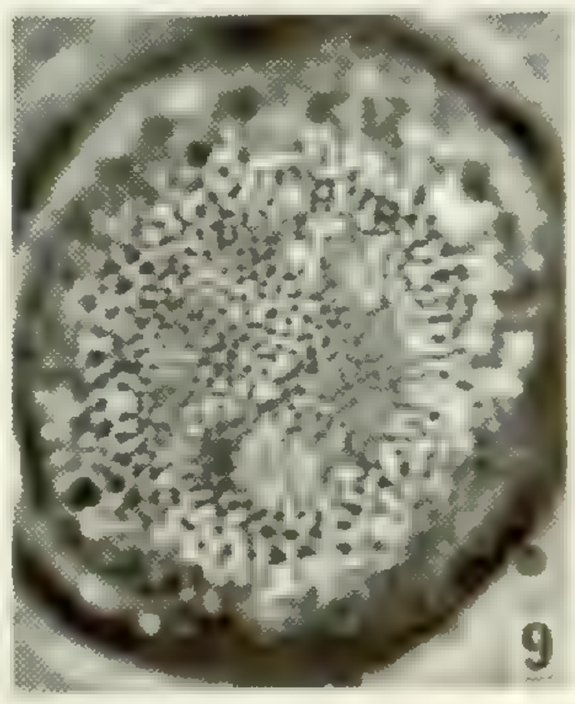


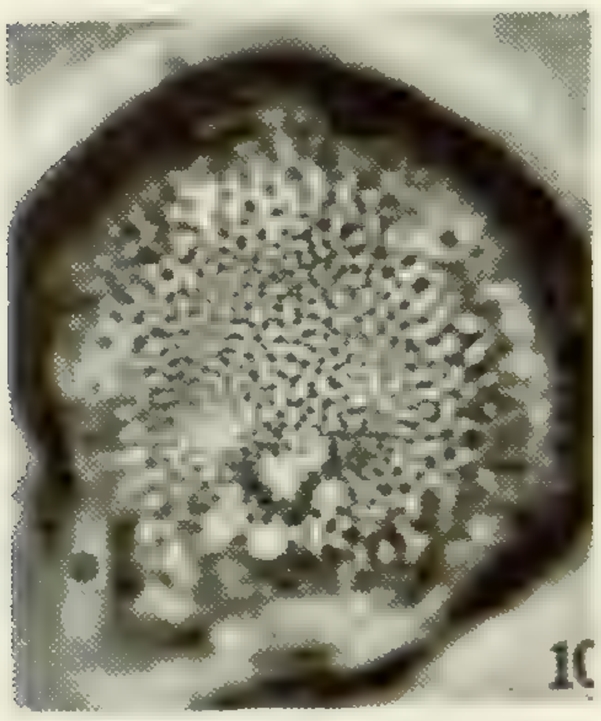


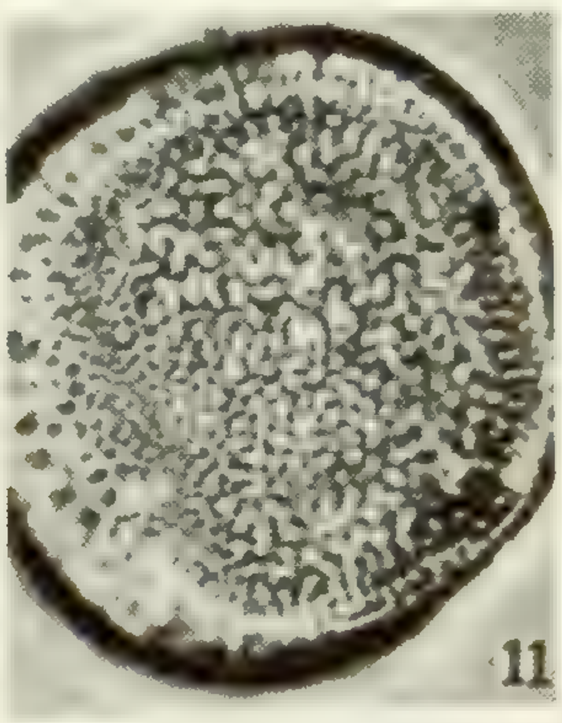












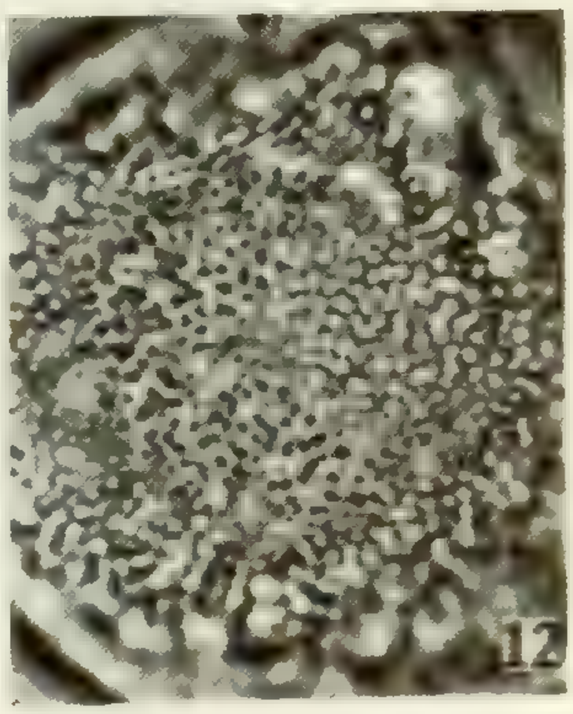


PLATE 43. FIG. 1. *Annona praetermissa* Fawc. & Rendle, × 500. FIG. 2,3. *A. pittieri* Donn. Smith; Fig. 2. × 200; Fig. 3, × 1000. FIG. 4,5. *A. macroprophyllata* Donn. Smith; Fig. 4, × 500; Fig. 5, × 1000. FIG. 6. *A. bullata* A. Rich., × 1000. FIG. 7. *A. crassivenia* Saff., × 1000. FIG. 8. *A. haitiensis* R. E. Fries. × 1000. FIG. 9. *A. rosei* Saff., × 1000. FIG. 10. *A. dumetorum* R. E. Fries. × 1000. FIG. 11. *A. bicolor* Urb., × 1000. FIG. 12. *A. globiflora* Schlecht., × 1000.

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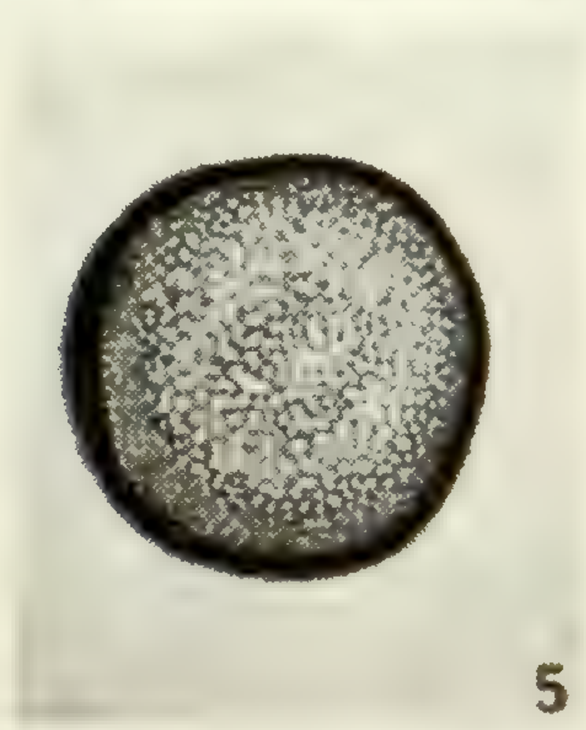
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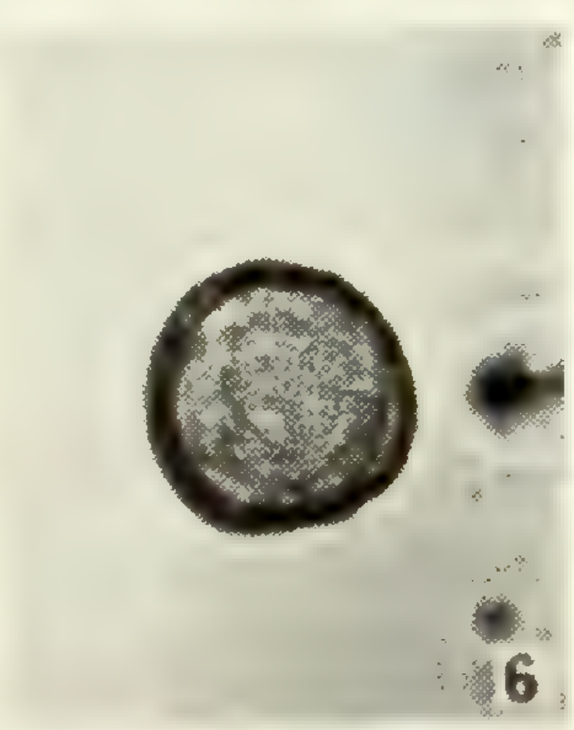
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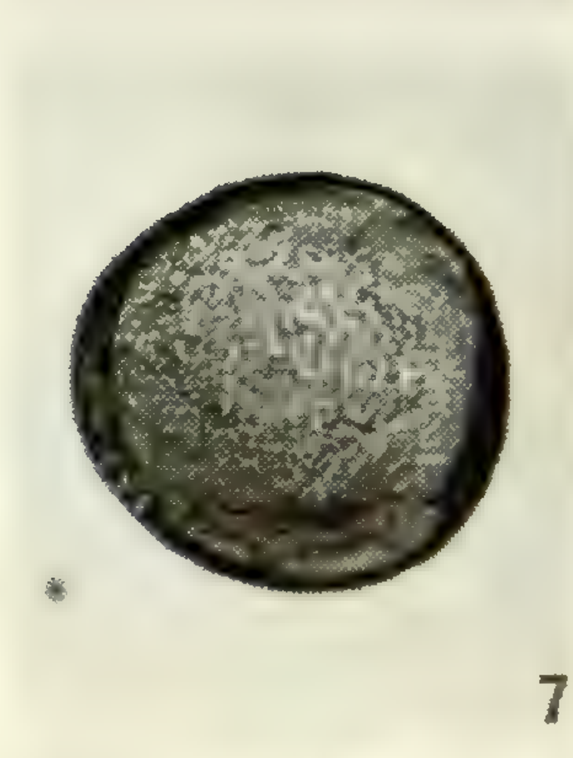
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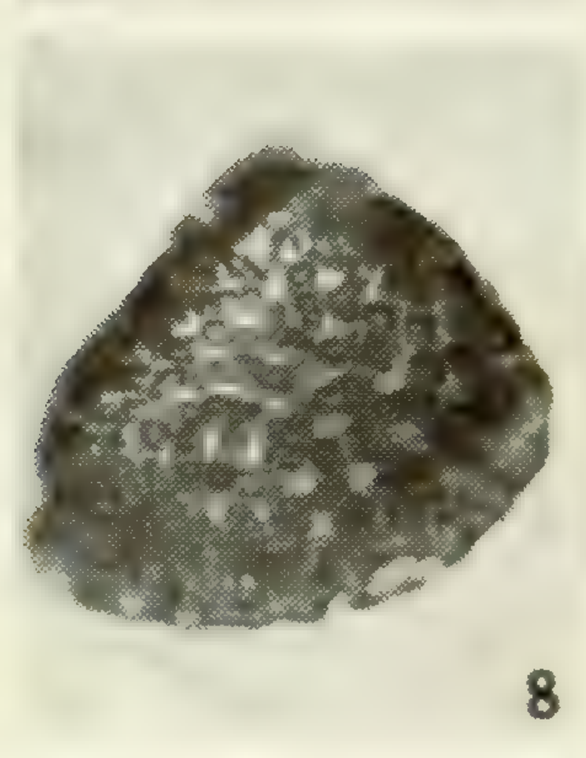
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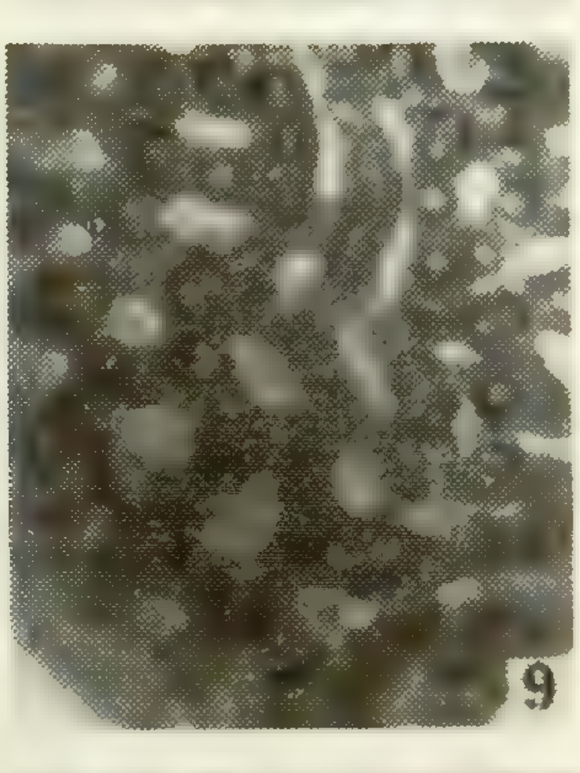
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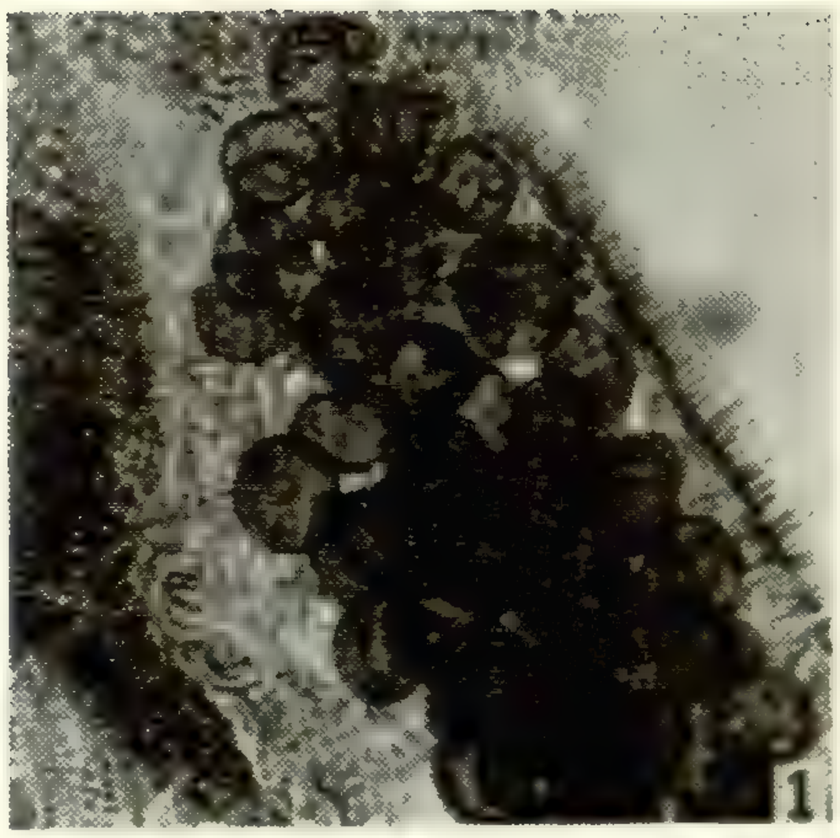
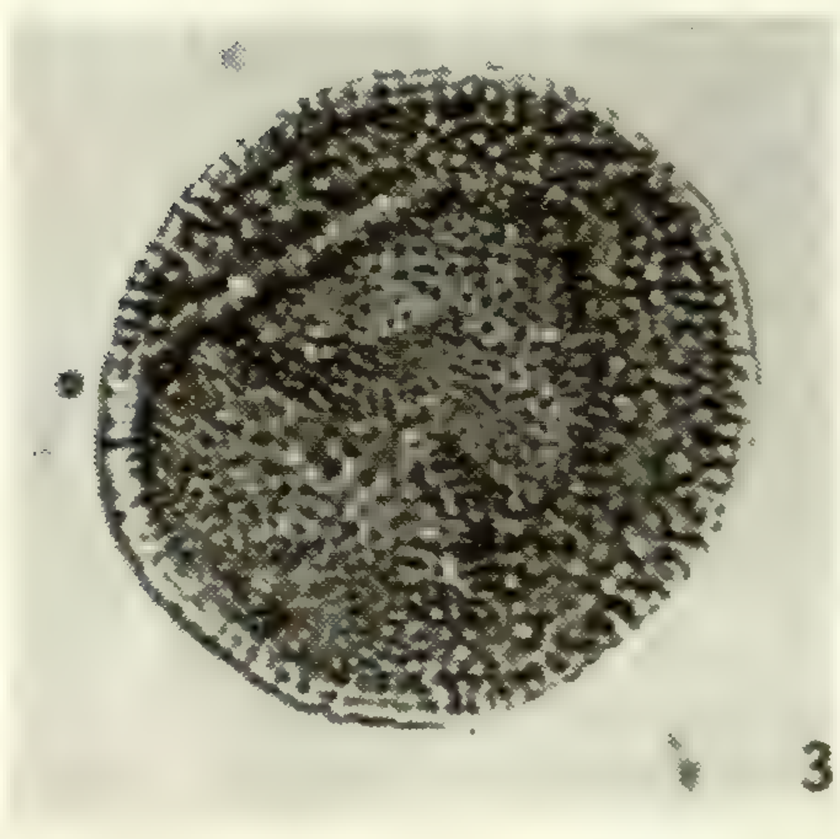
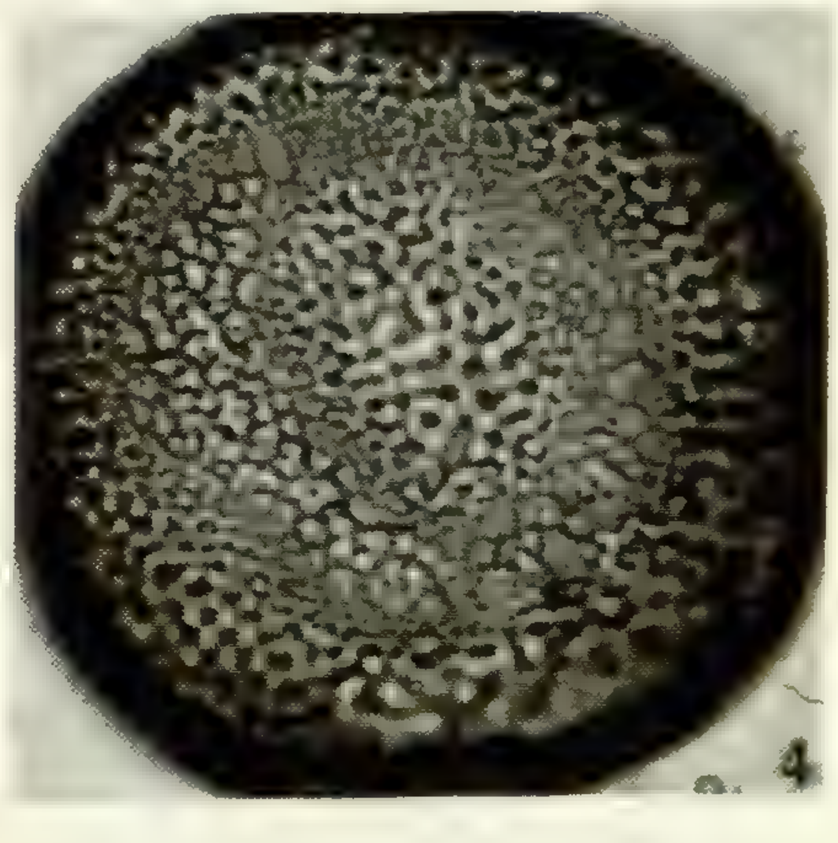
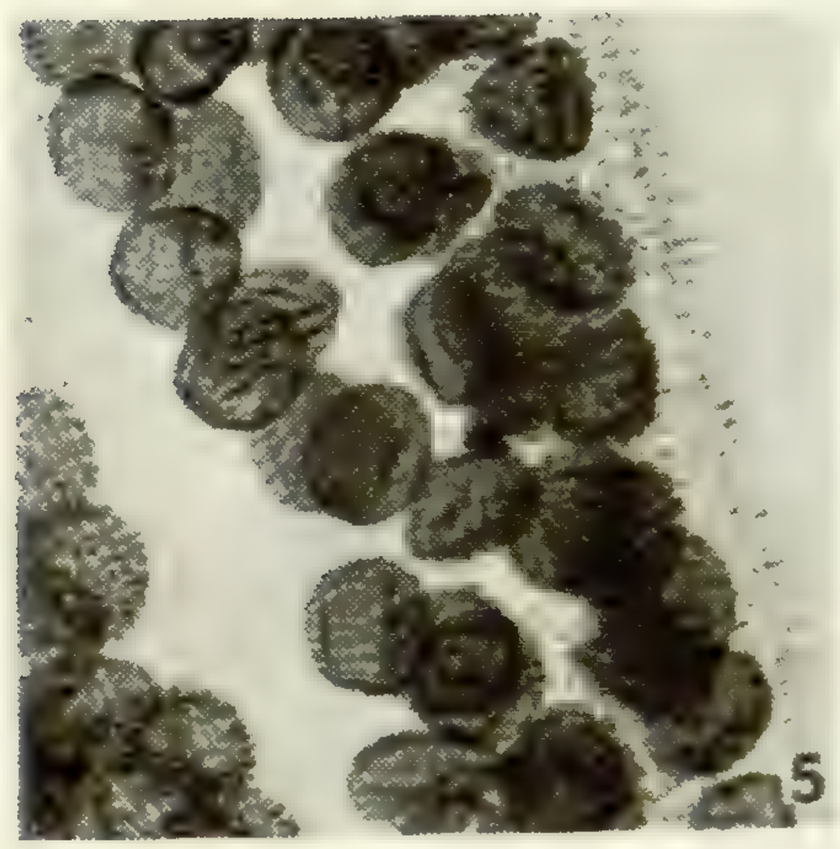
PLATE 44. FIG. 1,2. *Rollinia emarginata* Schlecht.; Fig. 1, × 500; Fig. 2, × 1000. FIG. 3. *R. intermedia* R. E. Fries, × 500. FIG. 4. *R. rigidiflora* R. E. Fries, × 500. FIG. 5. *R. sericea* R. E. Fries, × 500. FIG. 6. *R. microsepala* Standl., × 500. FIG. 7. *Rolliniopsis parviflora* (St. Hil.) Saff., × 500. FIG. 8,9. *Raimondia quinduensis* (HBK.) Saff.; Fig. 8, × 500; Fig. 9, × 1000. FIG. 10. *R. tenuiflora* (Mart.) R. E. Fries, × 500. FIG. 11. *Porcelia magnifructum* (Schery) R. E. Fries, × 500. FIG. 12. *Trigynaea oblongifolia* Schlecht., × 500.









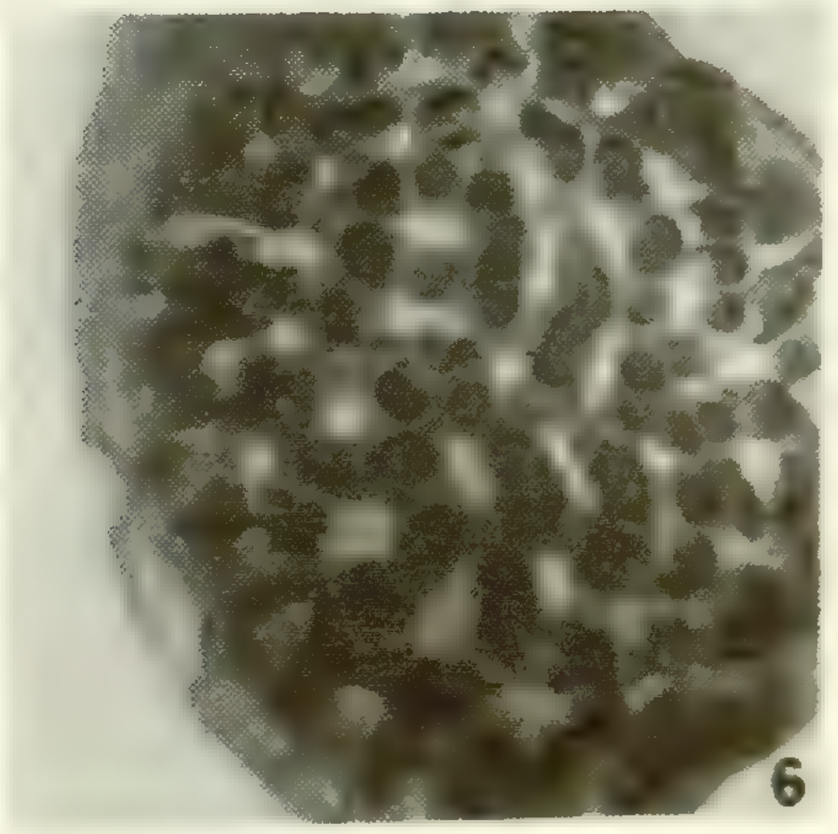
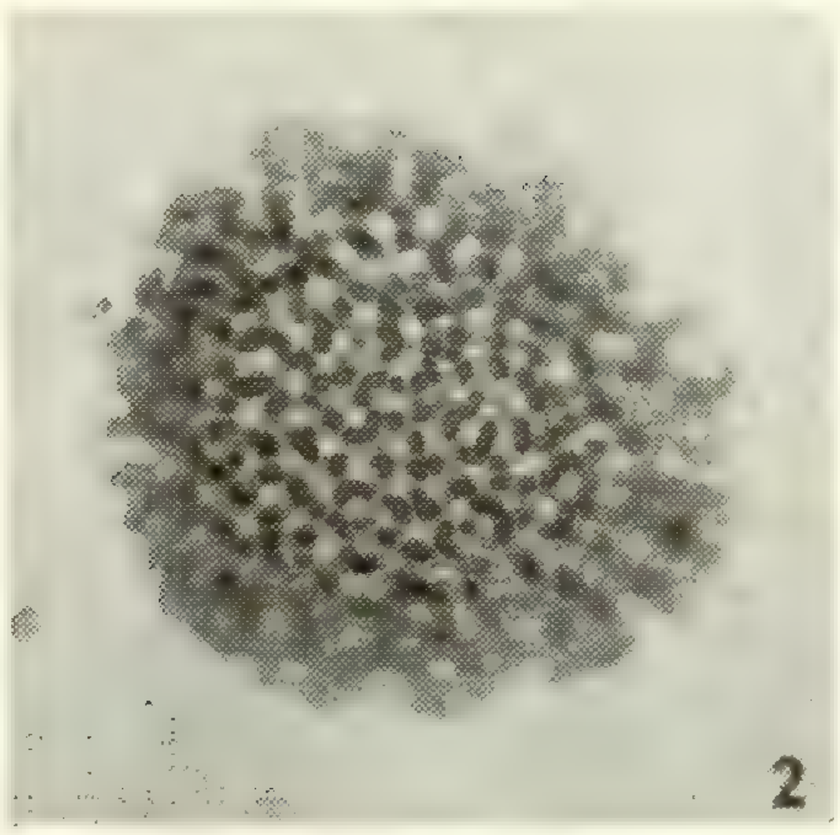


PLATE 45. FIG. 1. *Rollinia laurifolia* Schlecht., × 200. FIG. 2. *R. intermedia* R. E. Fries, × 200. FIG. 3. *R. rigidiflora* R. E. Fries, × 1000. FIG. 4. *R. sericea* R. E. Fries, × 1000. FIG. 5. *Rolliniopsis parviflora* (St. Hil.) Saff., × 200. FIG. 6. *Raimondia quinduensis* (HBK.) Saff., × 1000.

1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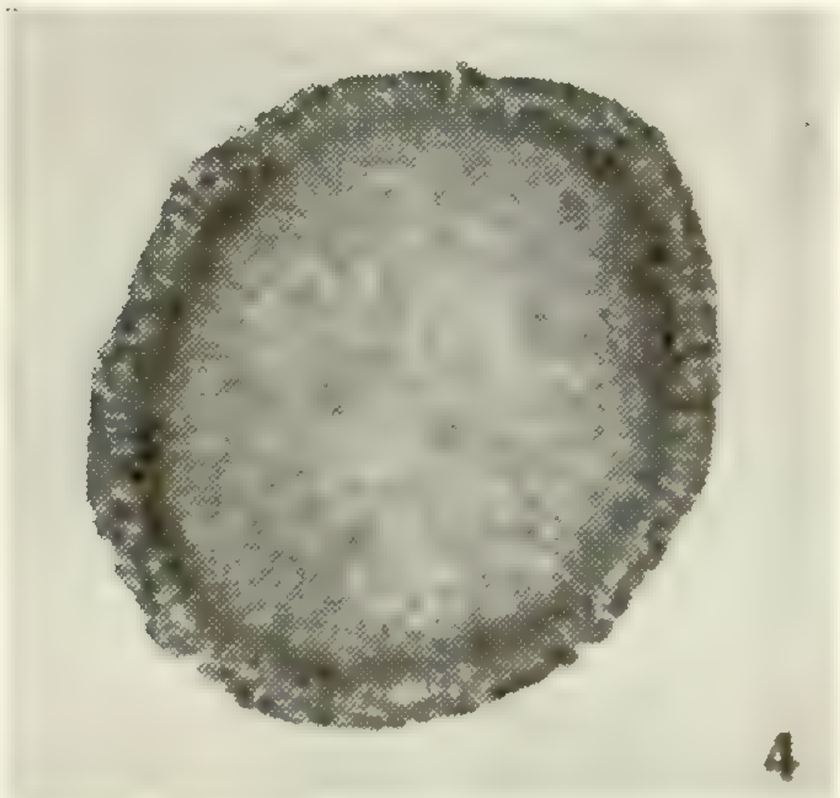
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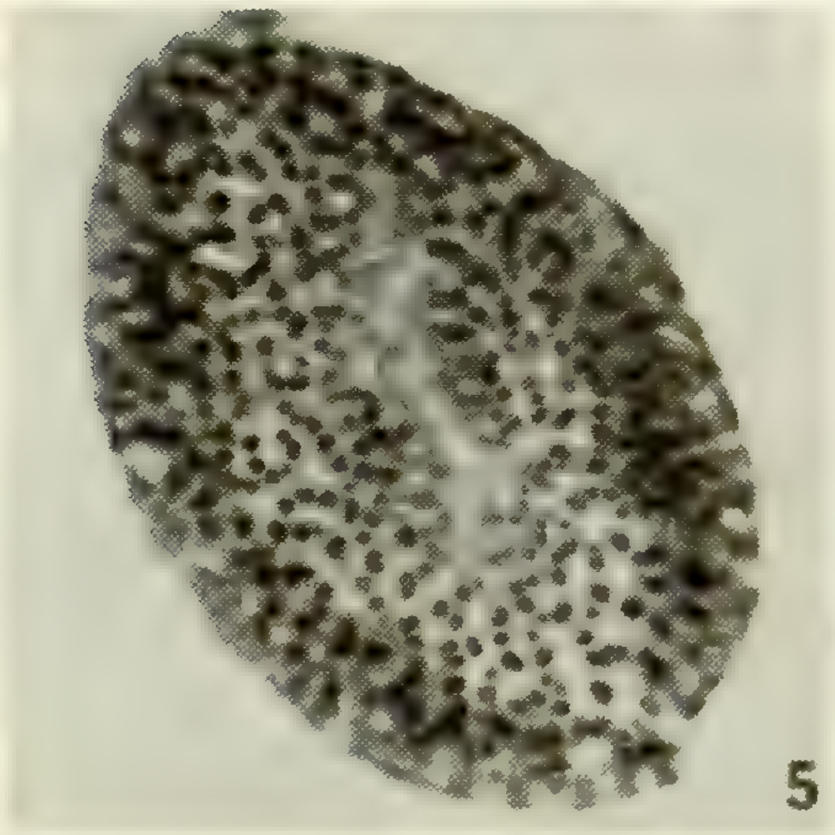
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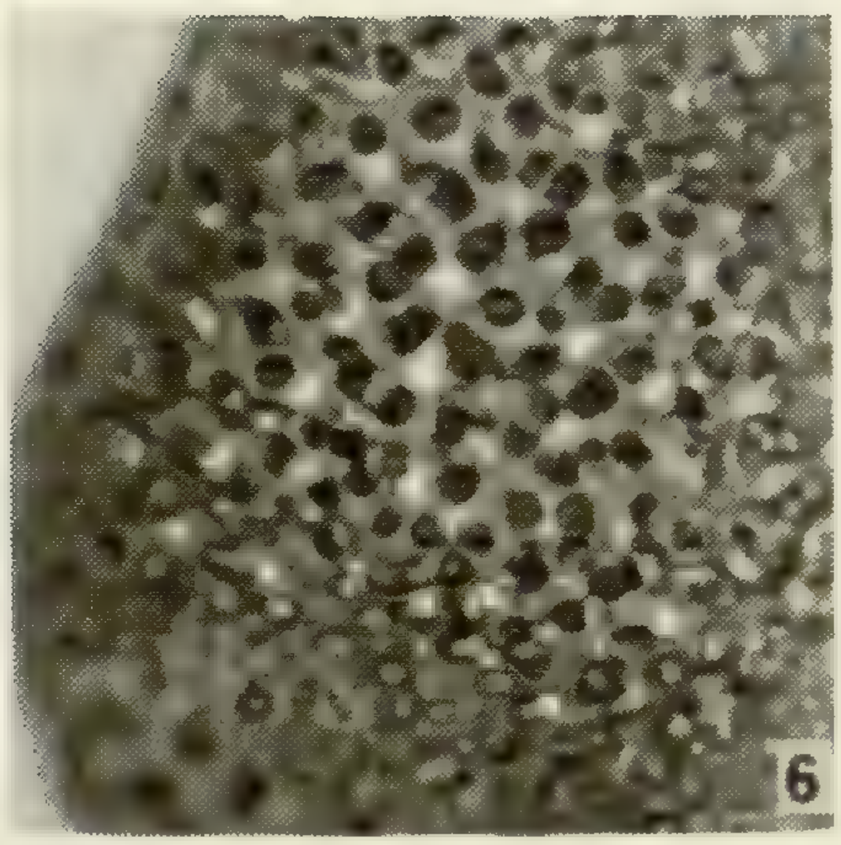
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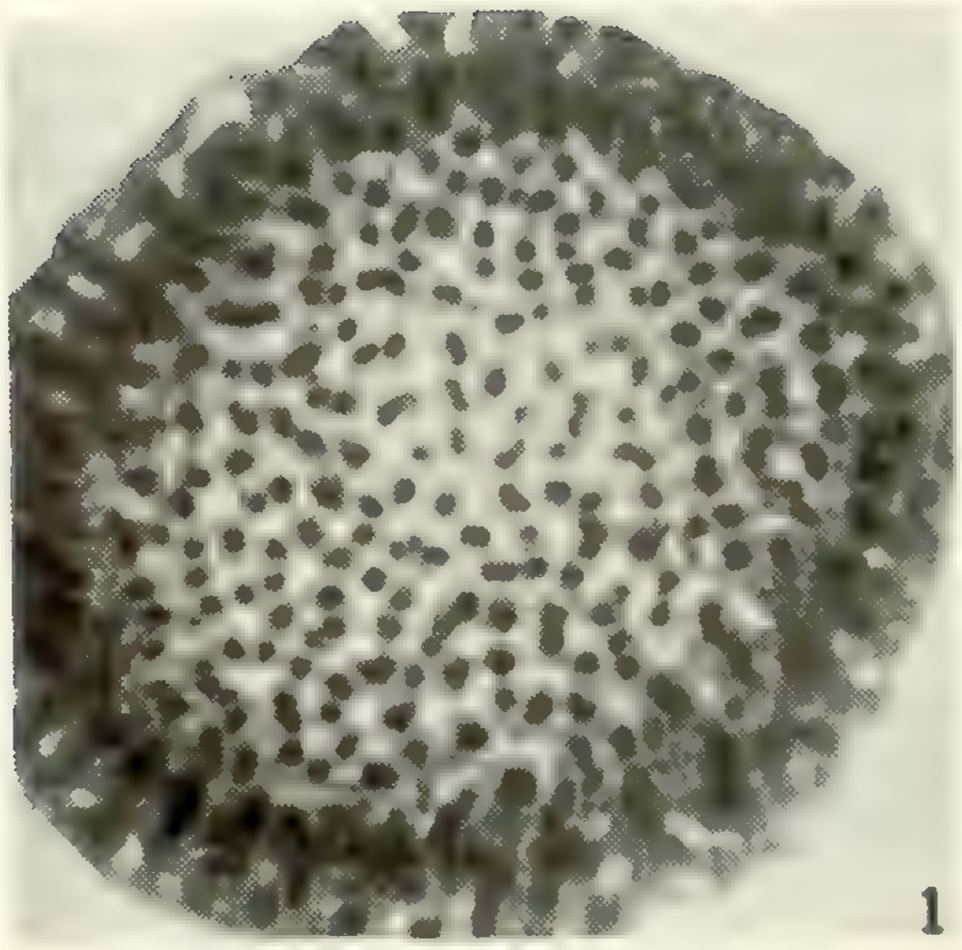
PLATE 46. FIG. 1. *Raimondia stenocarpa* R. E. Fries, × 500. FIG. 2. *Cymbopetalum baillonii* R. E. Fries, × 200. FIG. 3,4. *C. brasiliense* (Vell.) Benth., × 200. FIG. 5. *C. lanugipetalum* Schery, × 200. FIG. 6. *Cardiopetalum calophyllum* Schlecht., × 1000.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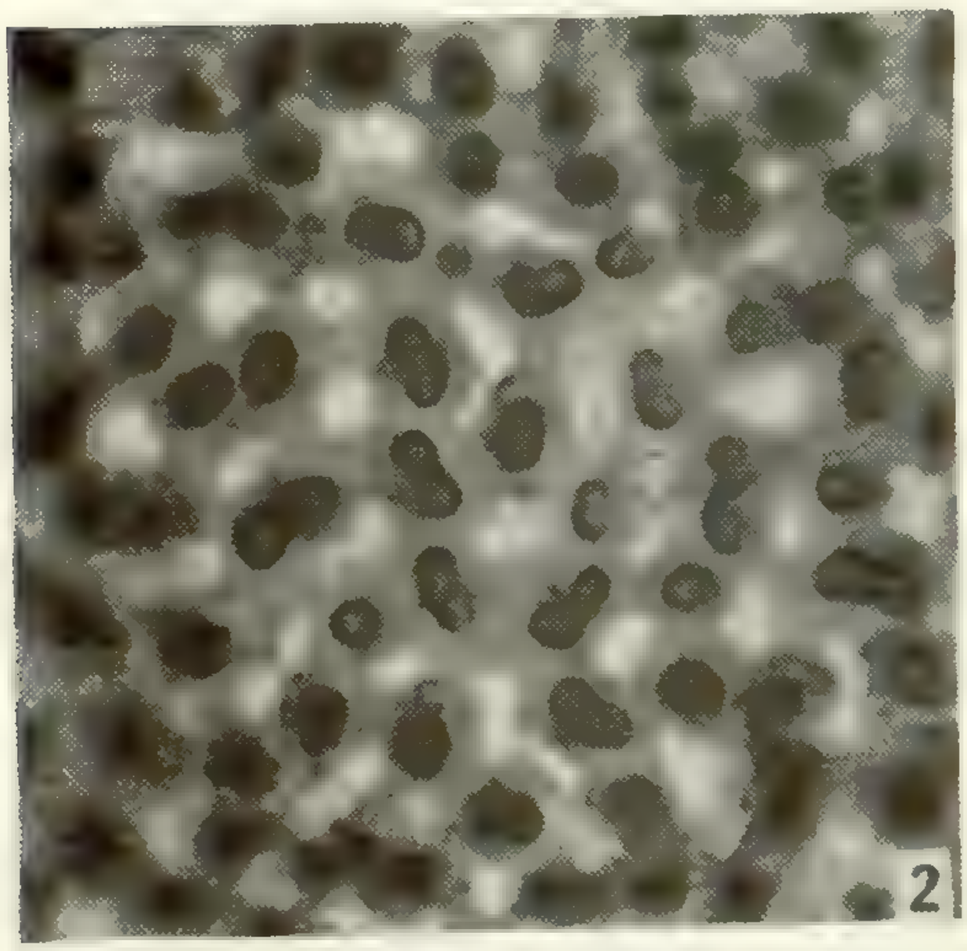
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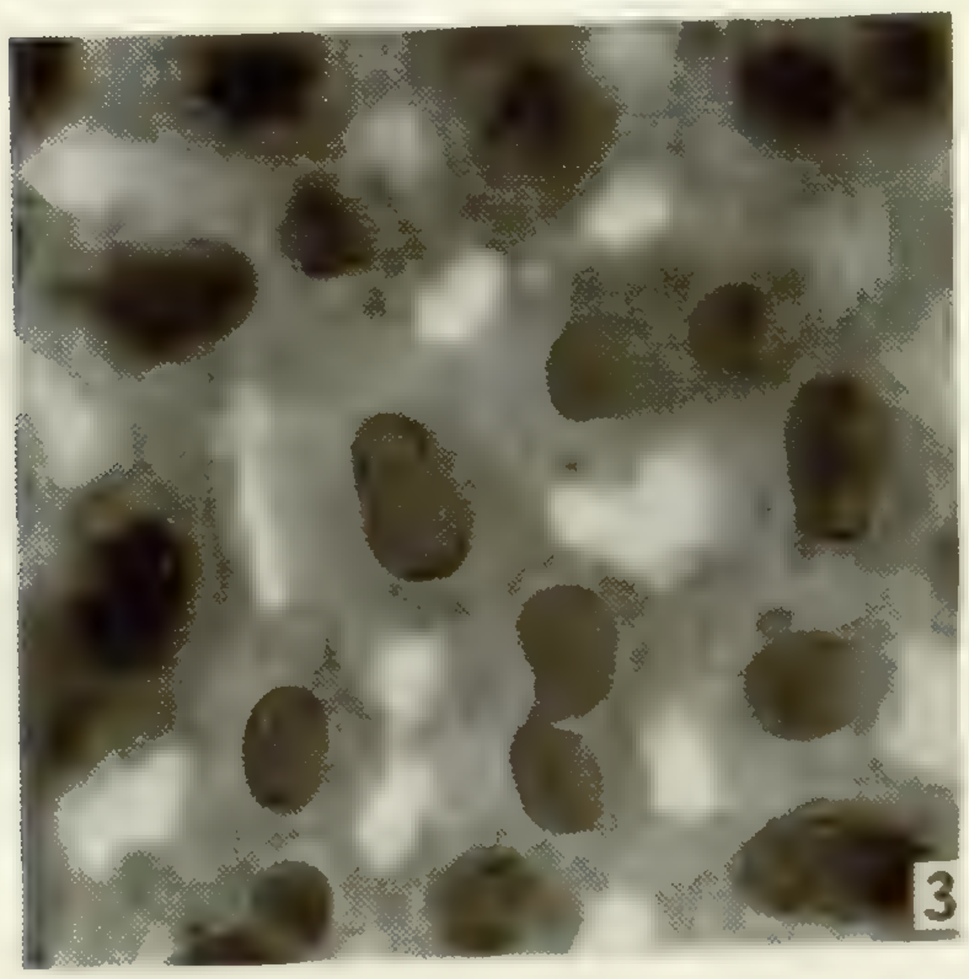
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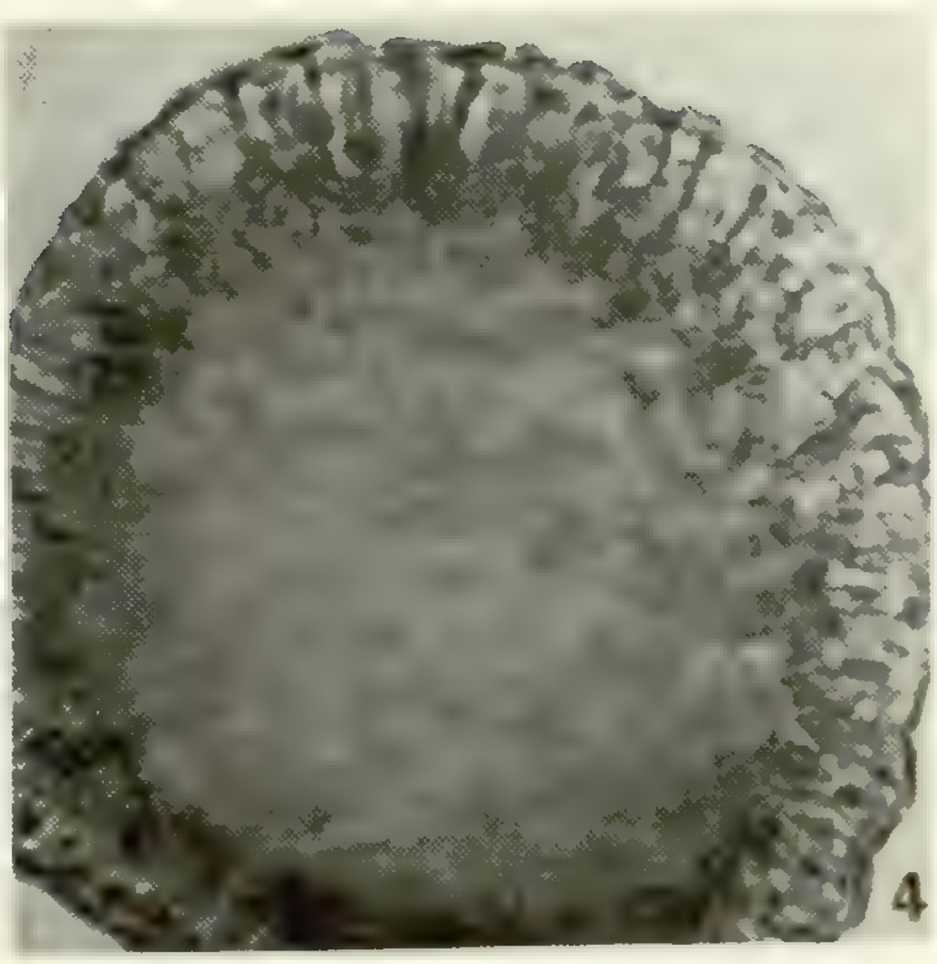
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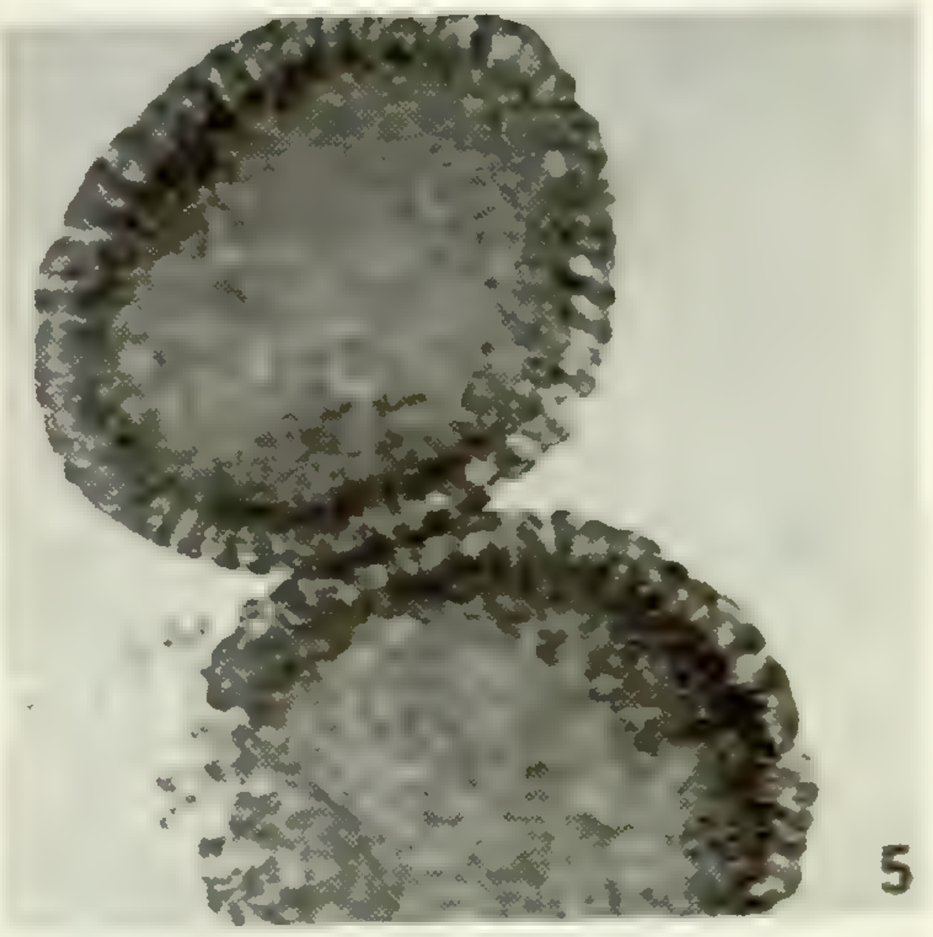
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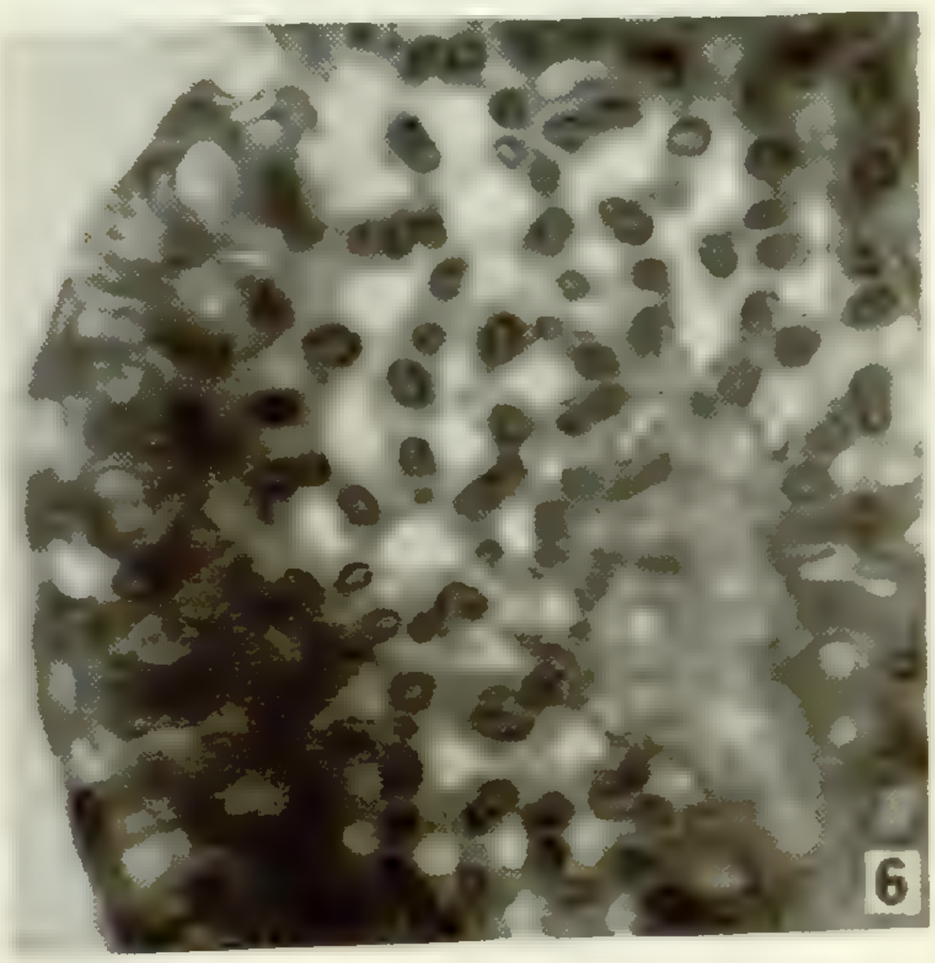
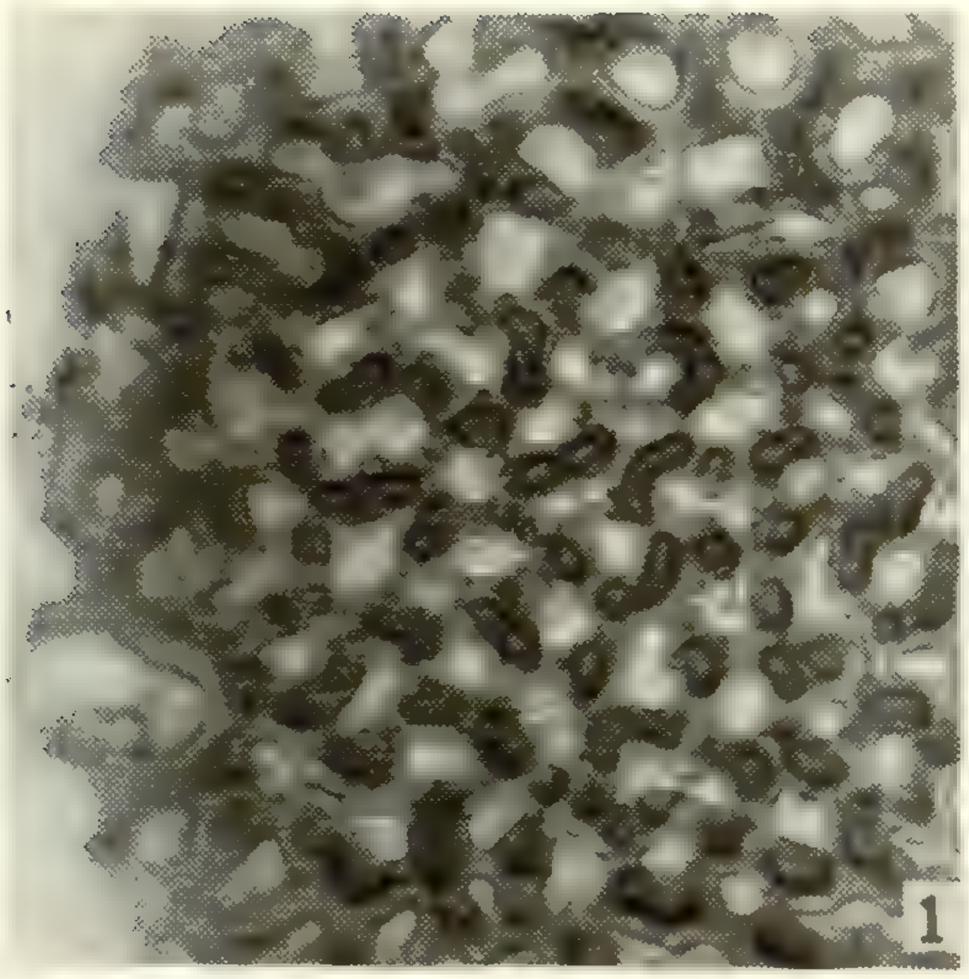
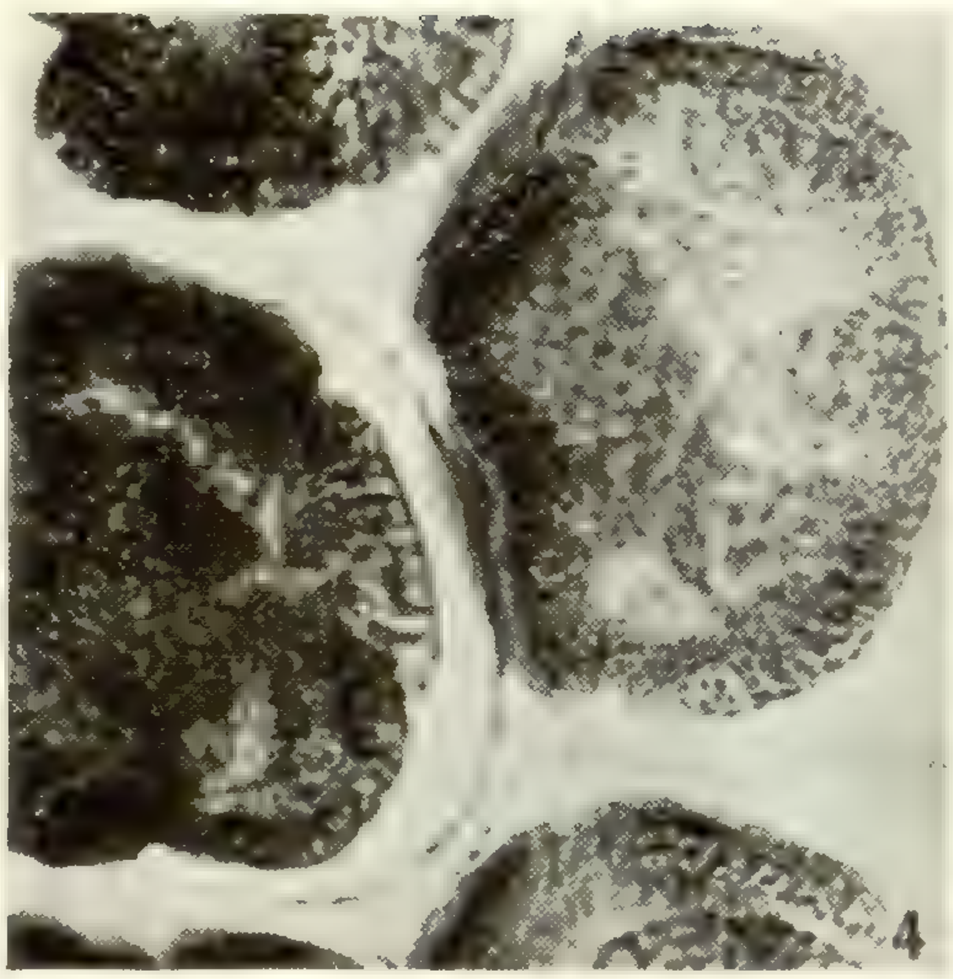
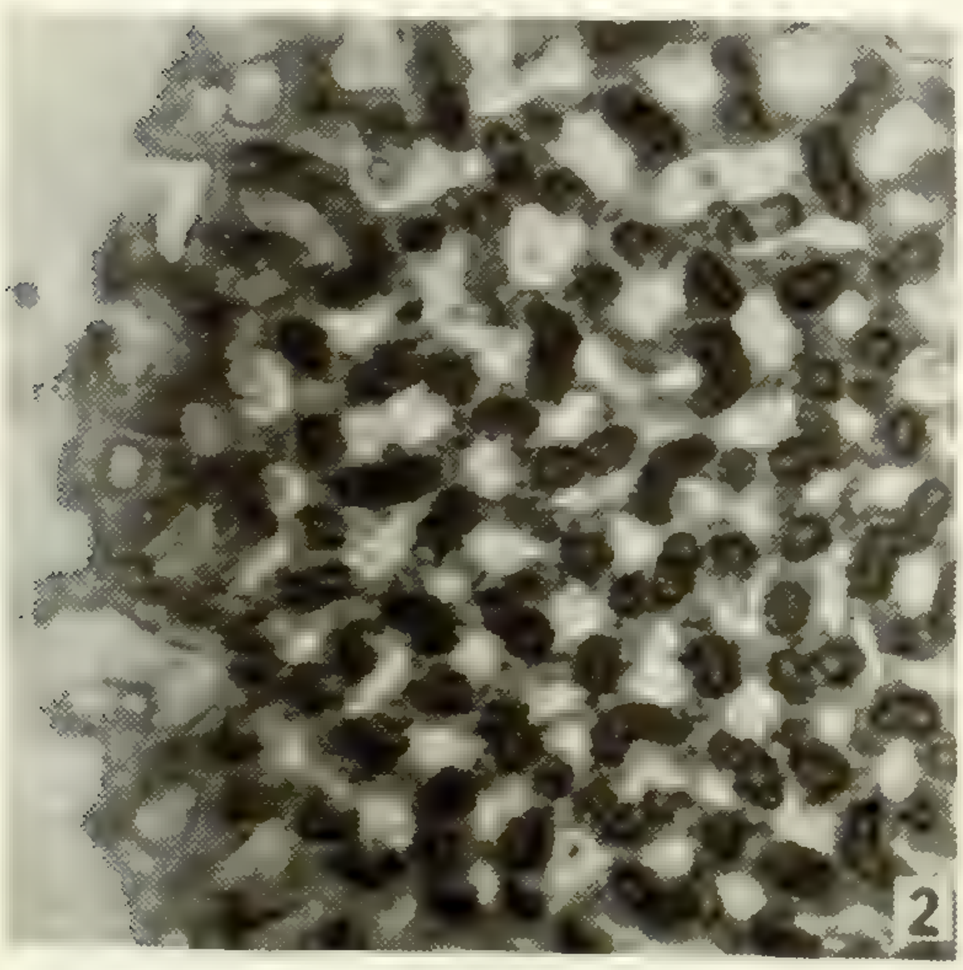
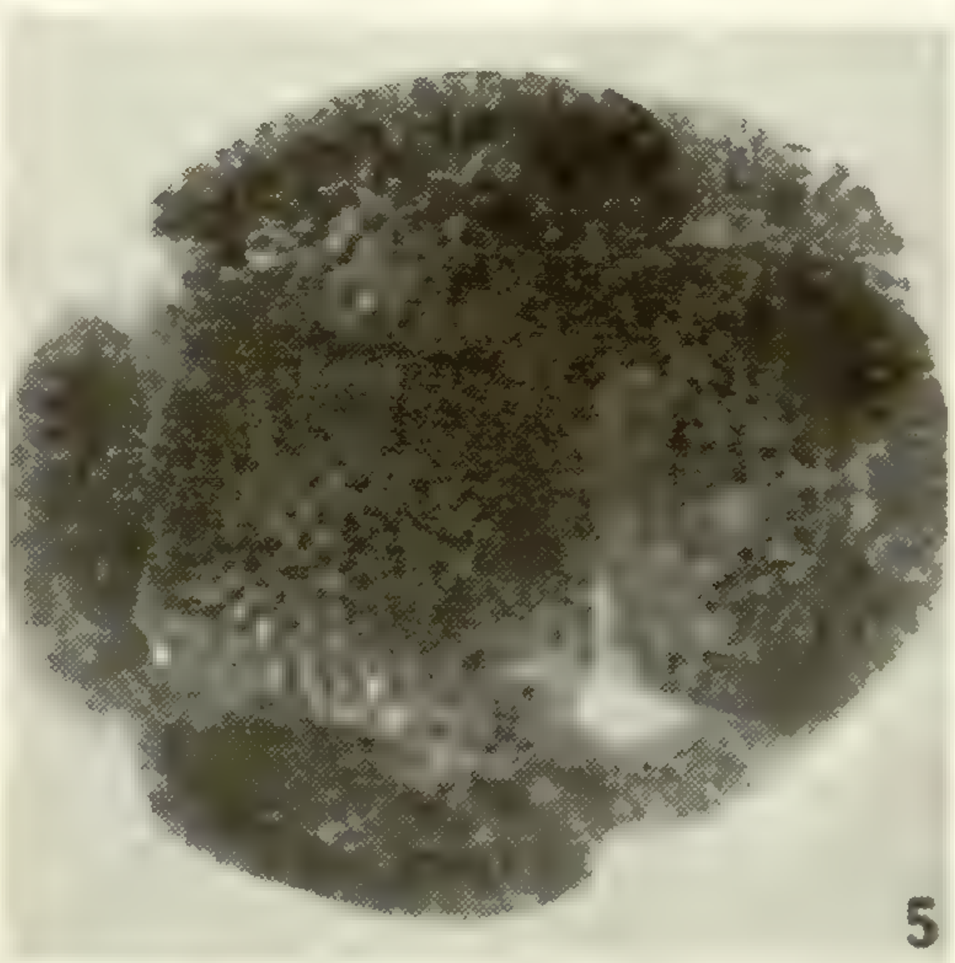

6

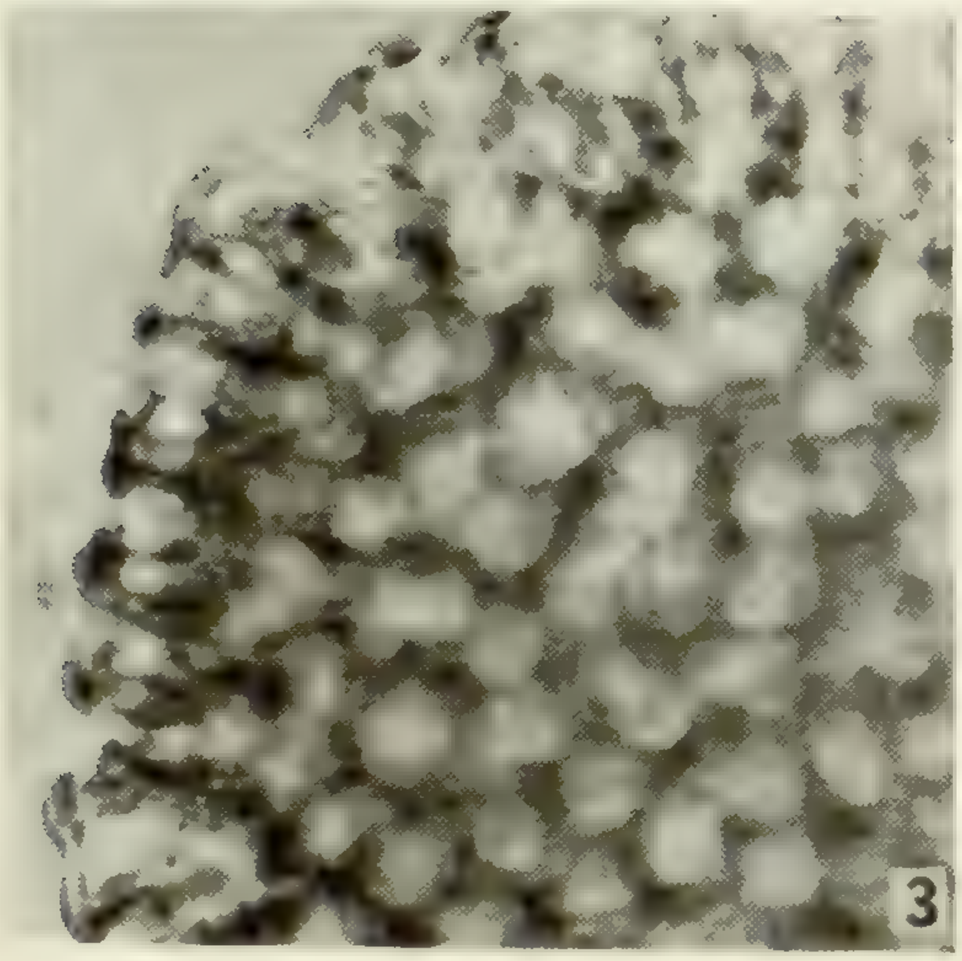
PLATE 47. FIG. 1–3. *Cymbopetalum odoratissimum* Barb. Rodr.; Fig. 1, × 200; Fig. 2, × 500; Fig. 3, × 1000. FIG. 4. *C. stenophyllum* Donn. Smith, × 500. FIG. 5. *C. baillonii* R. E. Fries. × 200. FIG. 6. *C. lanugipetalum* Schery, × 500.











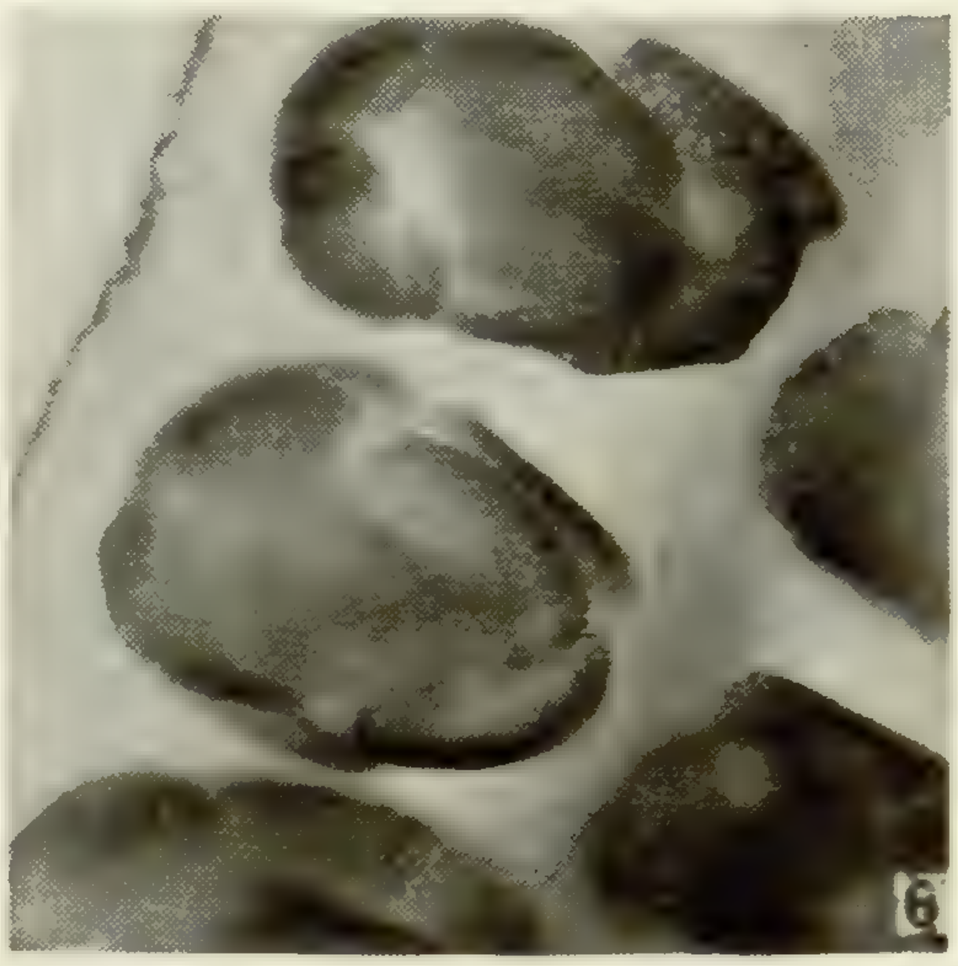
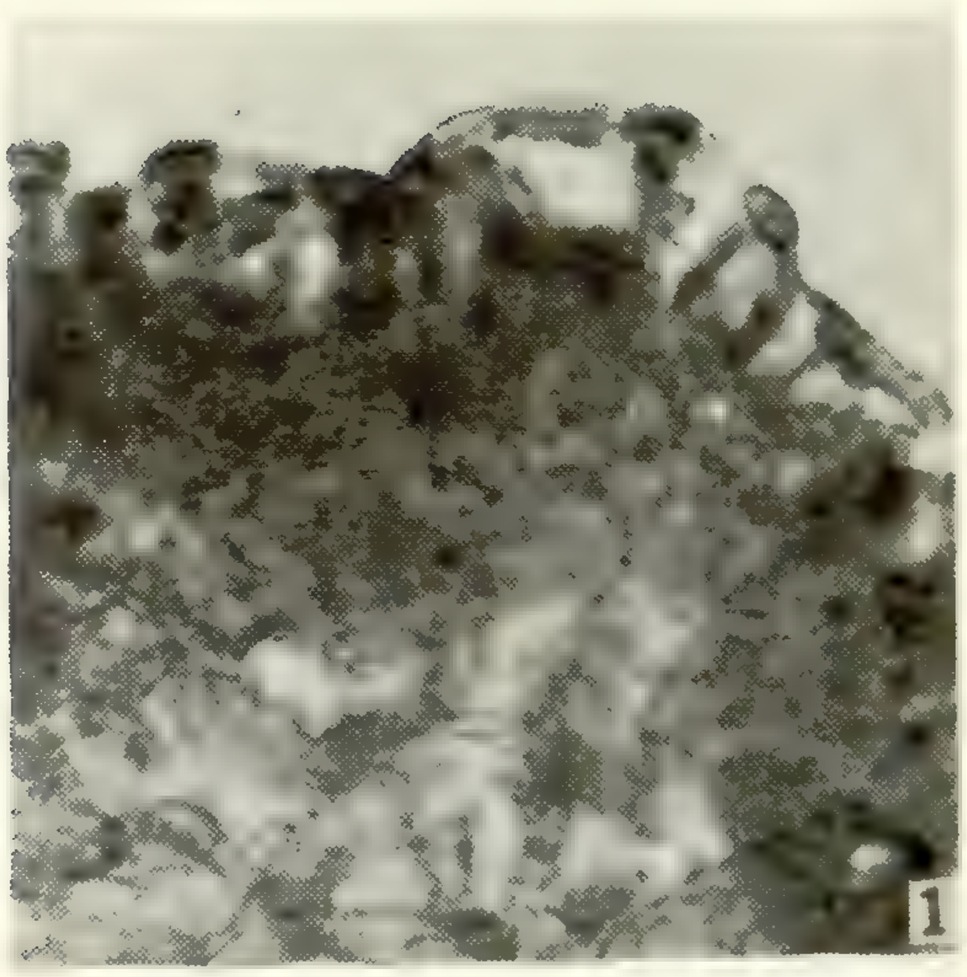
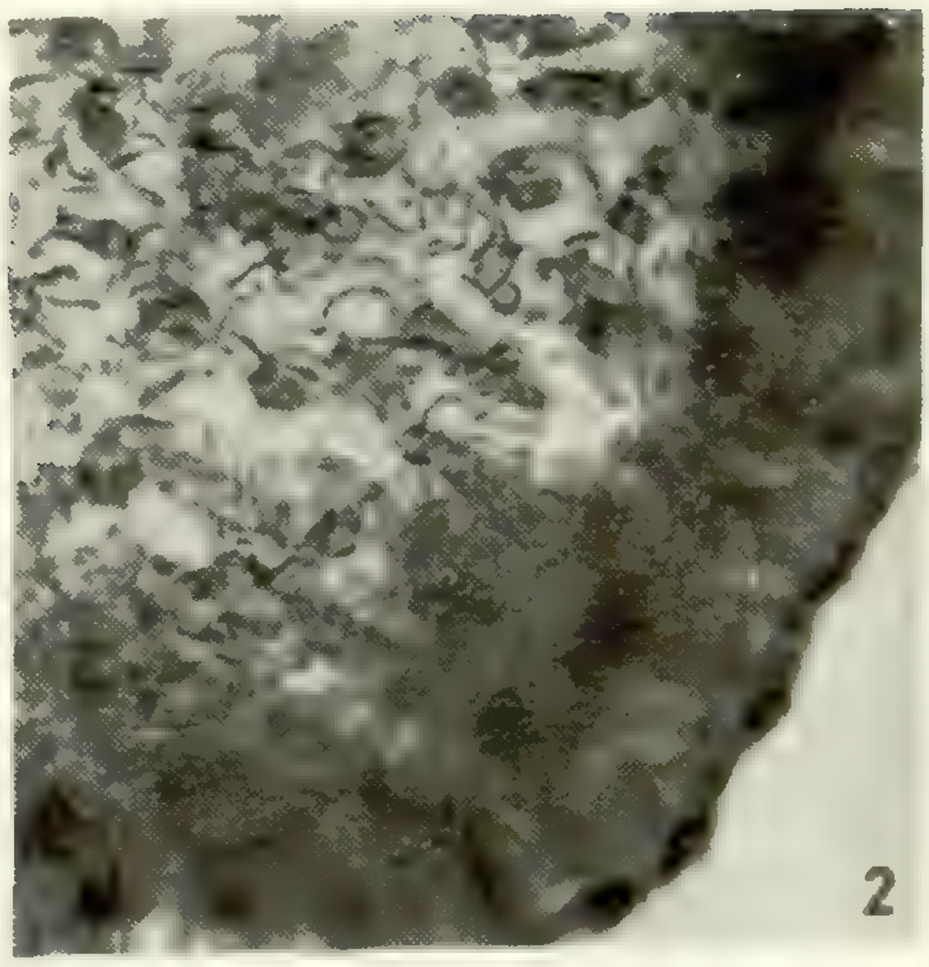
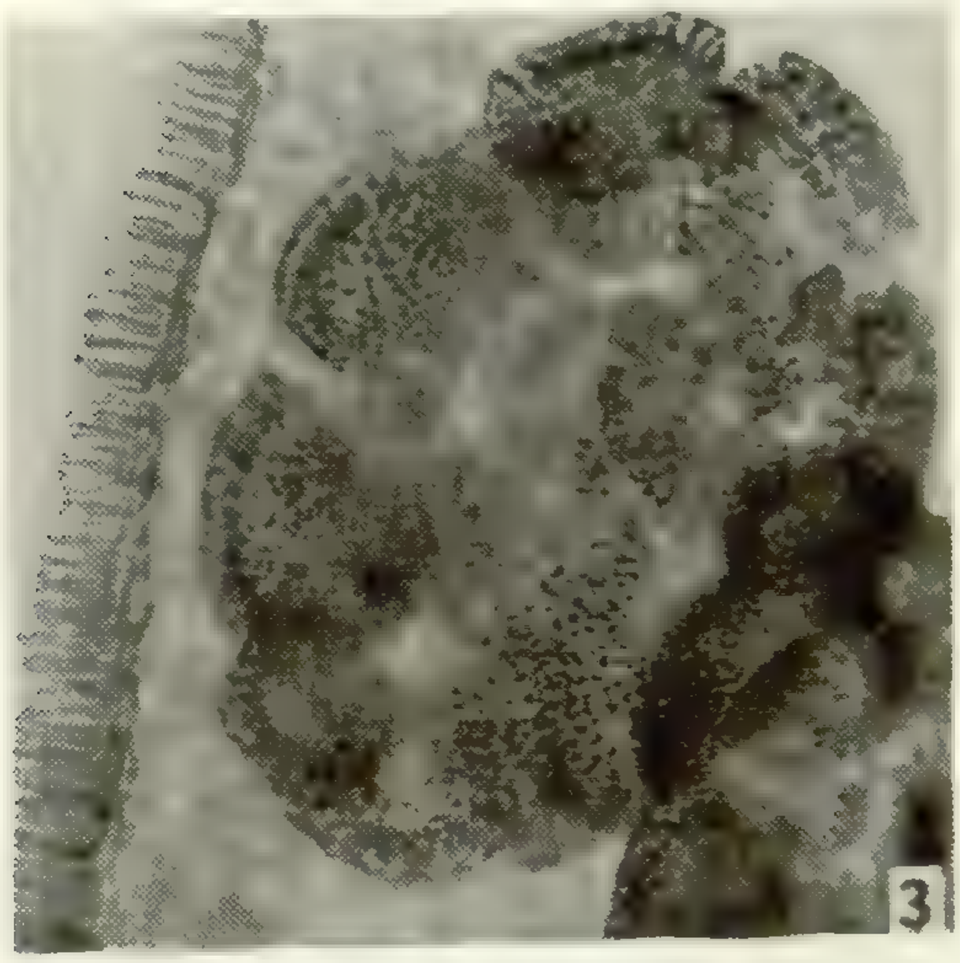
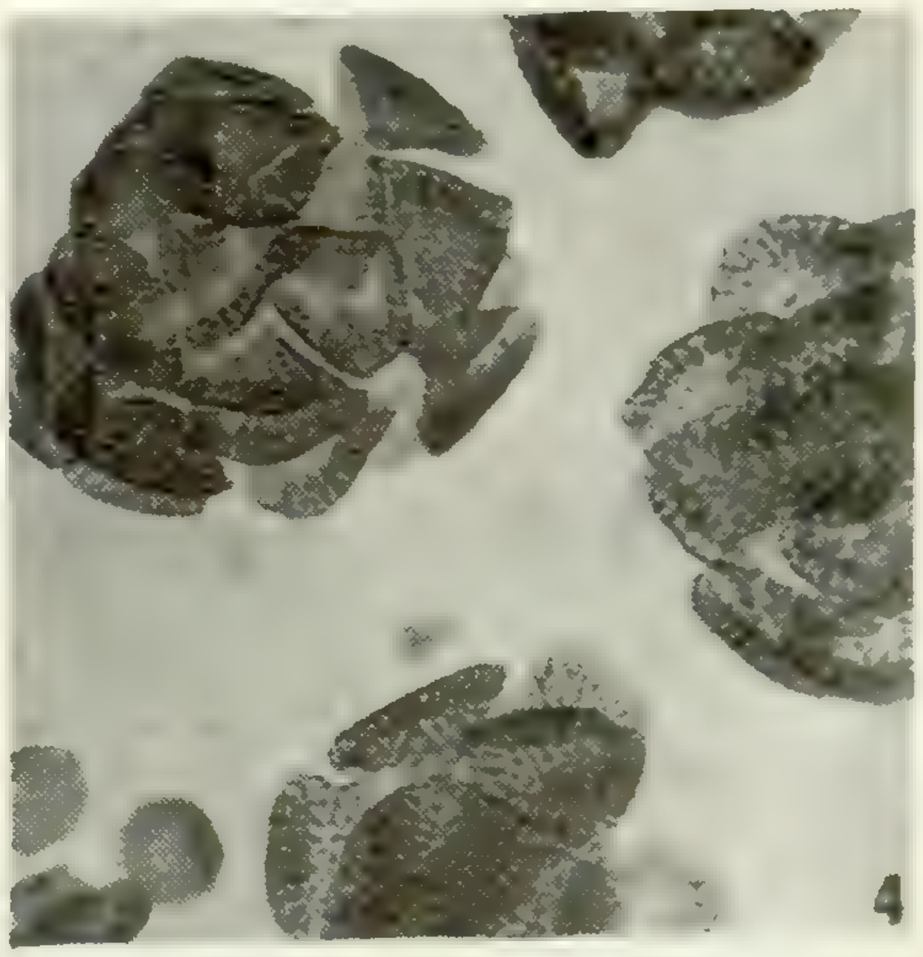


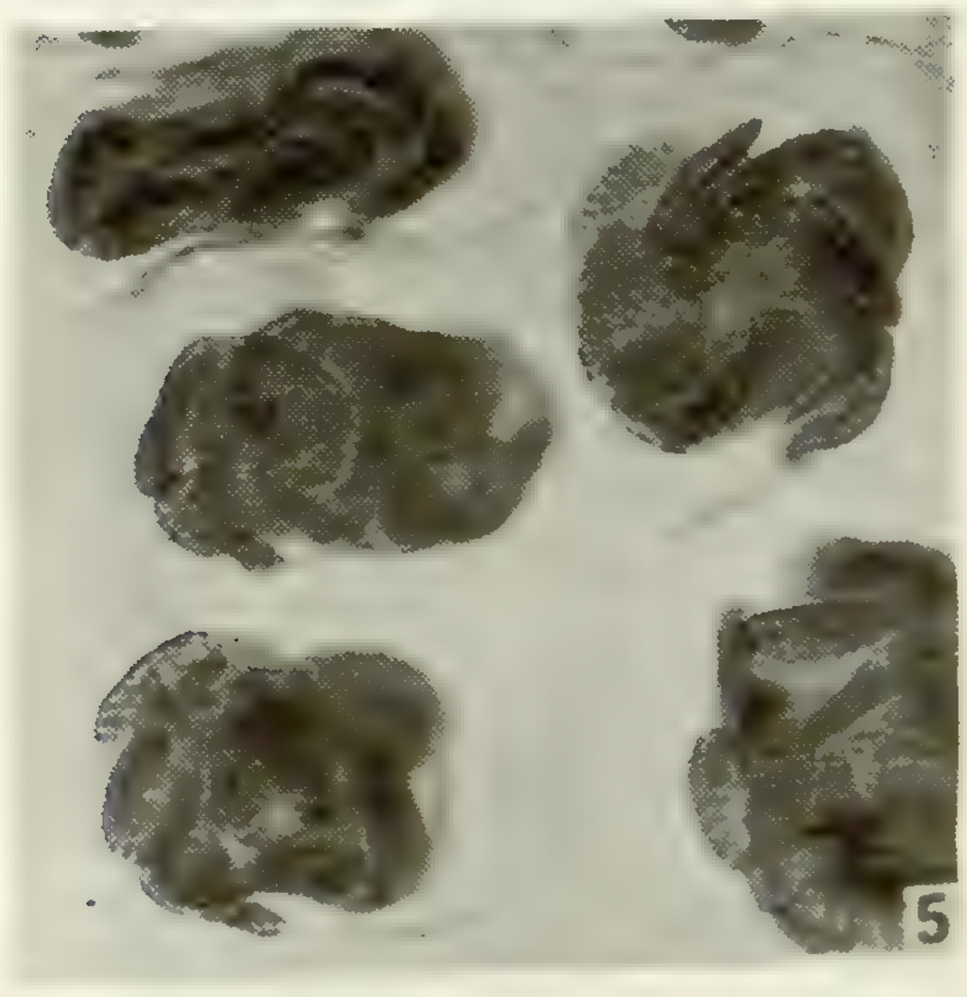
PLATE 48. FIG. 1–3. *Cymbopetalum baillonii* R. E. Fries, × 500. FIG. 4,5. *C. gracile* R. E. Fries, × 200. FIG. 6. *Cardiopetalum calophyllum* Schlecht., × 200.











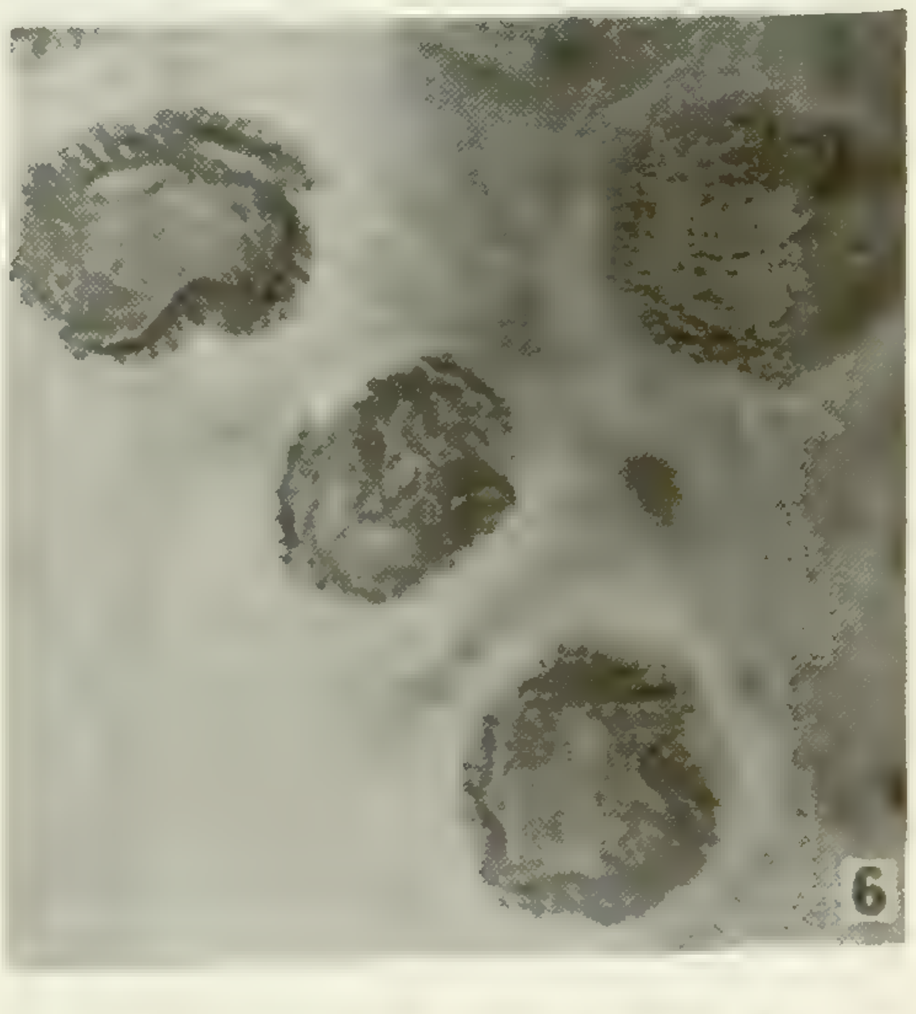
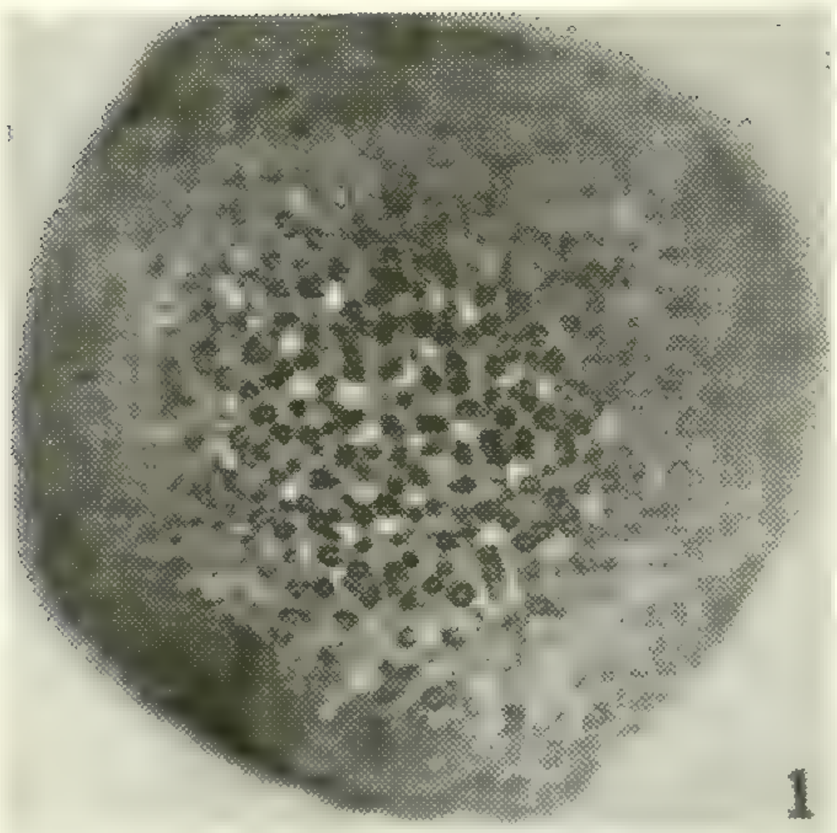
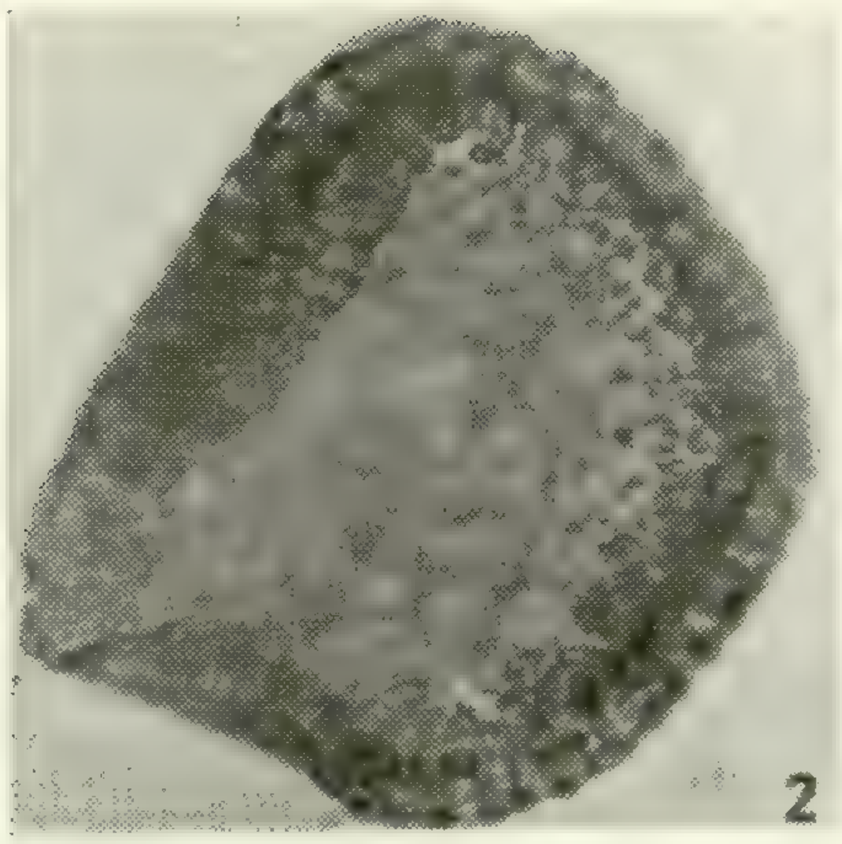
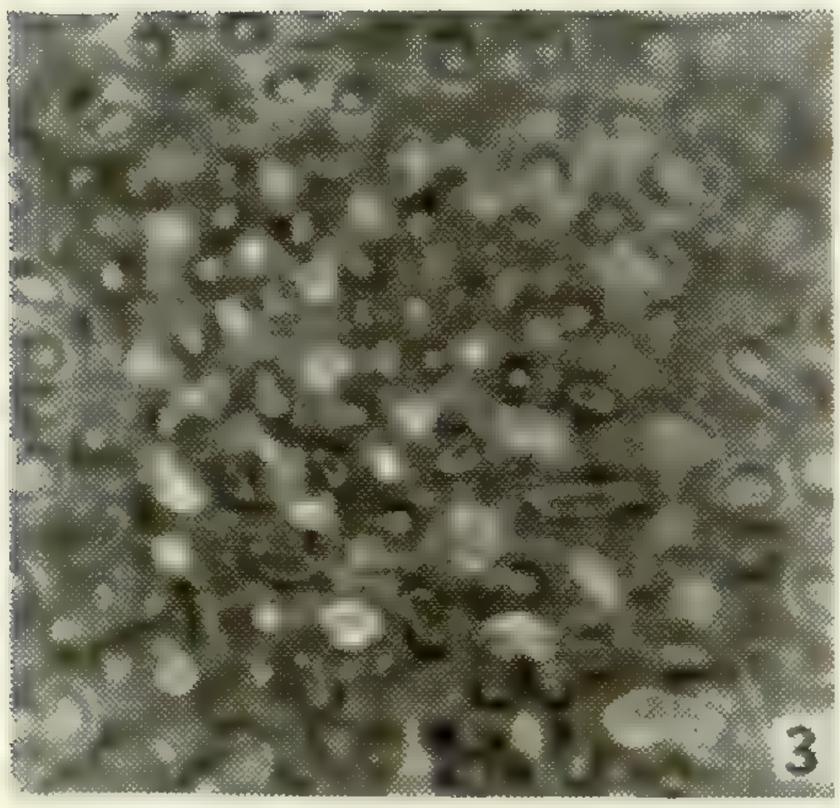
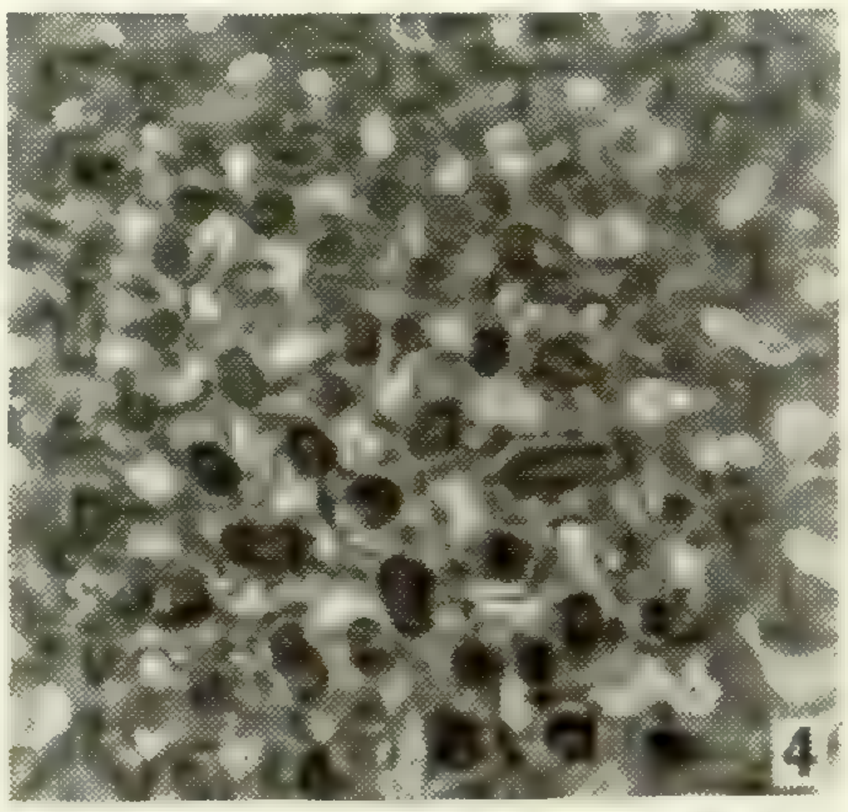


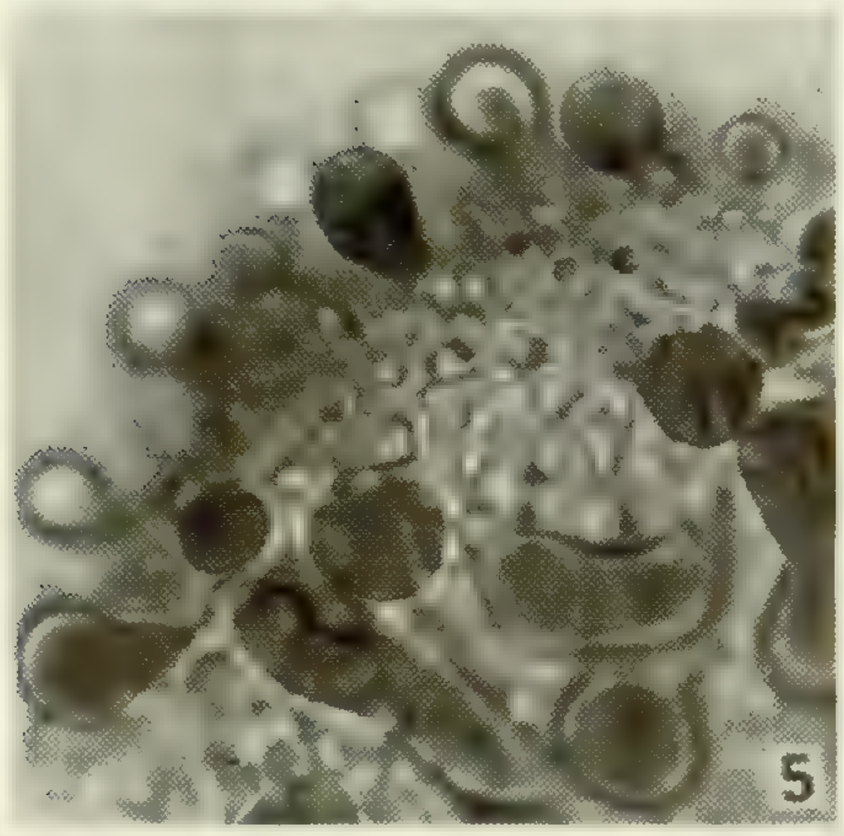
PLATE 49. FIG. 1,2. *Cymbopetalum longipes* (Benth.) Diels, × 500. FIG. 3. *Porcelia macrocarpa* (Warm.) R. E. Fries, × 200. FIG. 4. *P. nitidifolia* Ruiz & Pav., × 200. FIG. 5. *P. steinbachii* (Diels) R. E. Fries, × 200. FIG. 6. *Trigynaea oblongifolia* Schlecht., × 200.











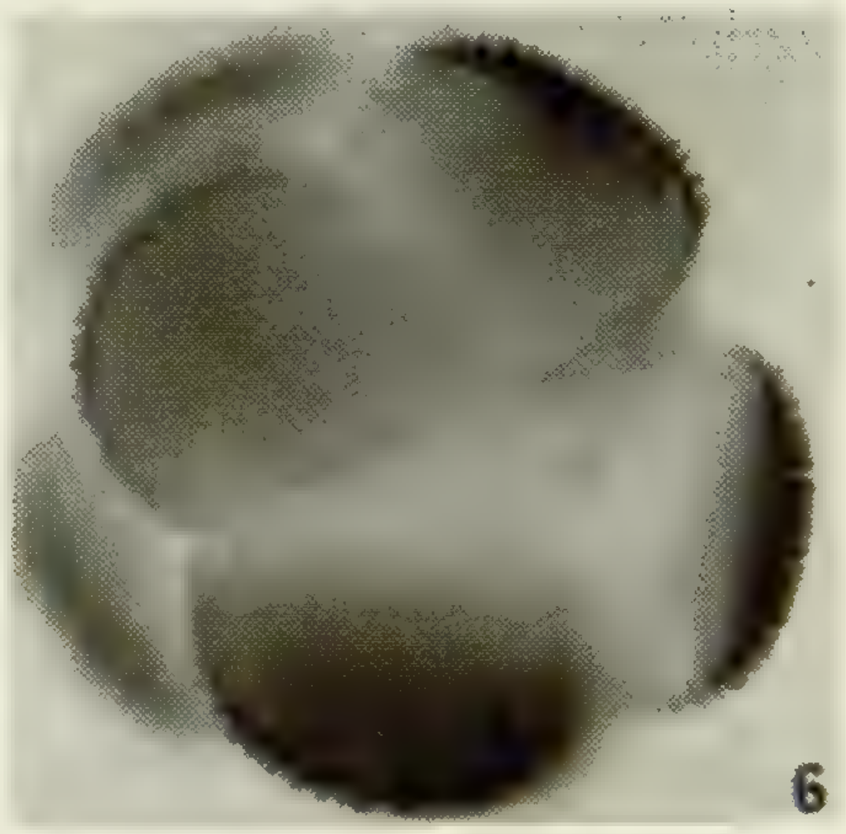
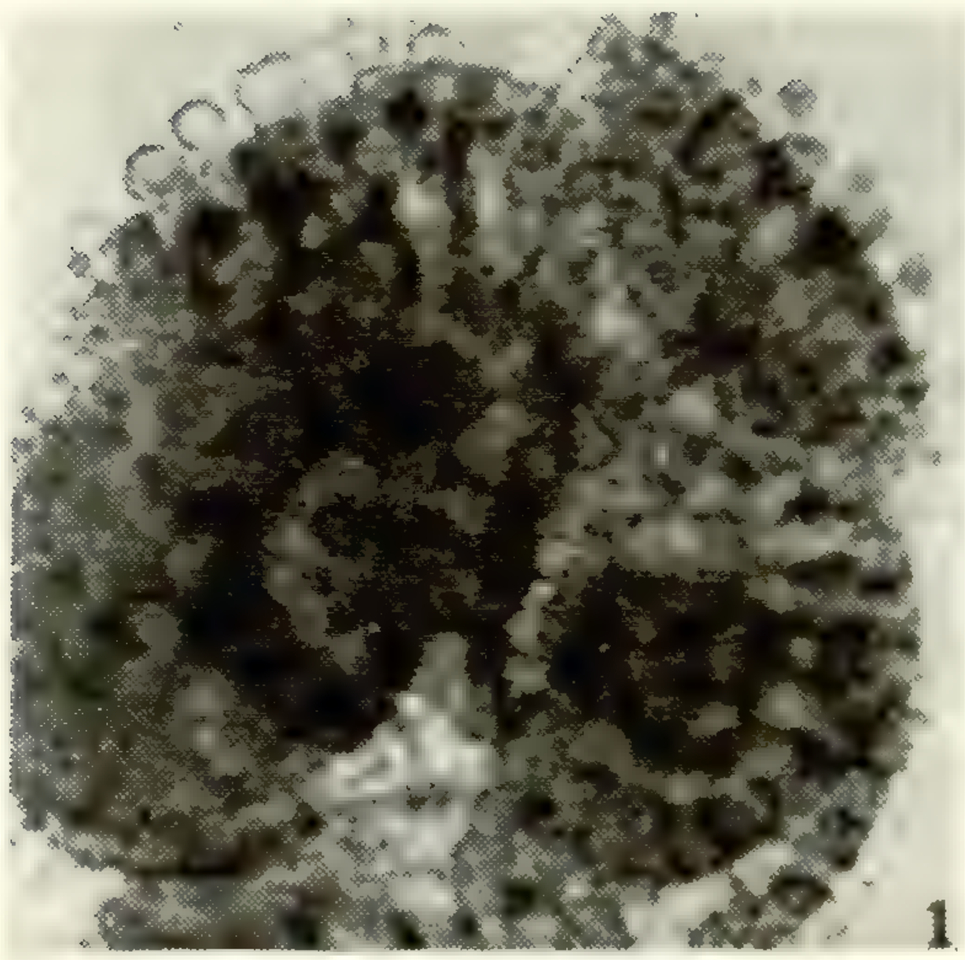
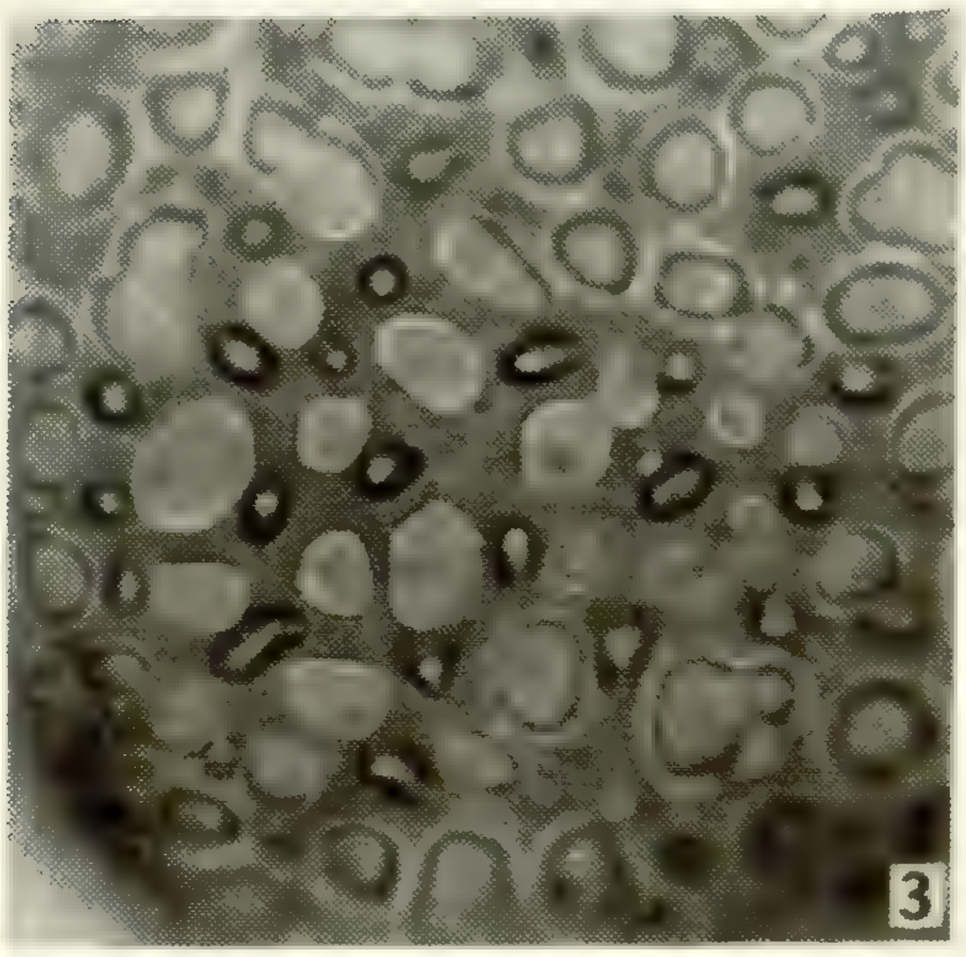
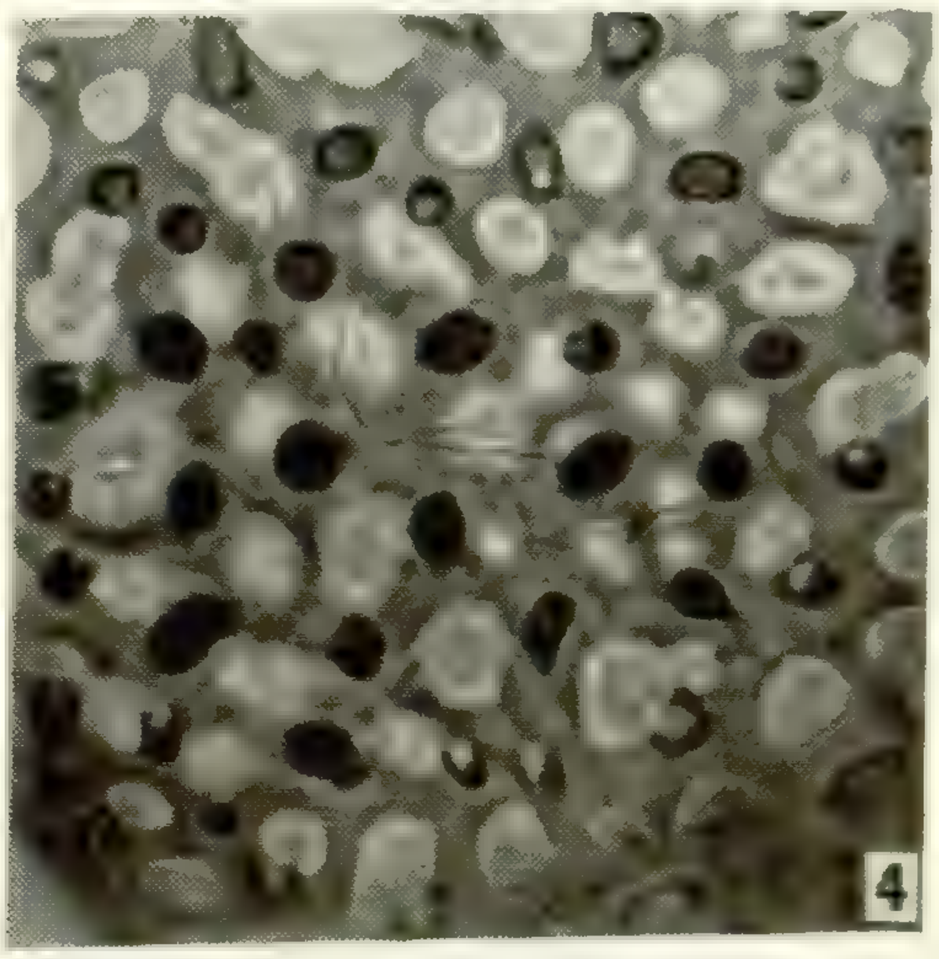


PLATE 50. FIG. 1,2. *Cardiopetalum calophyllum* Schlecht., × 500. FIG. 3,4. *Porcelia macrocarpa* (Warm.) R. E. Fries, × 1000. FIG. 5. *Trigynaea oblongifolia* Schlecht., × 1000. FIG. 6. *T. caudata* (R. E. Fries) R. E. Fries, × 500.







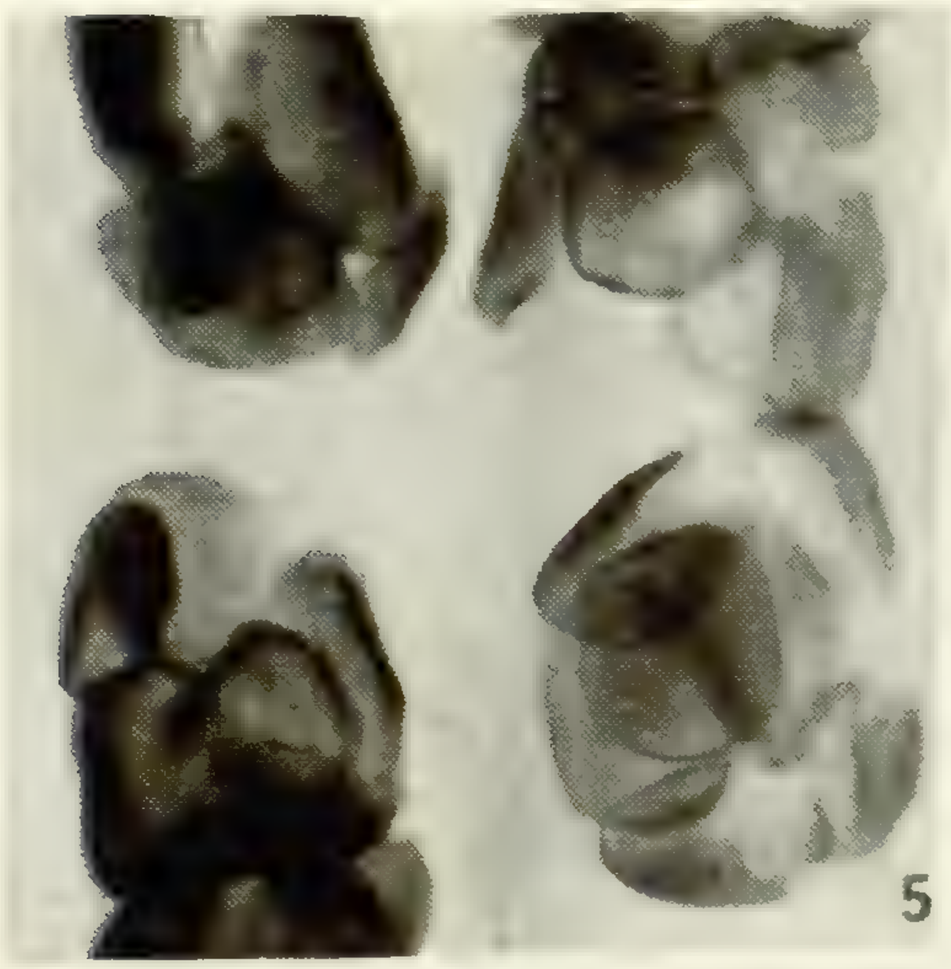
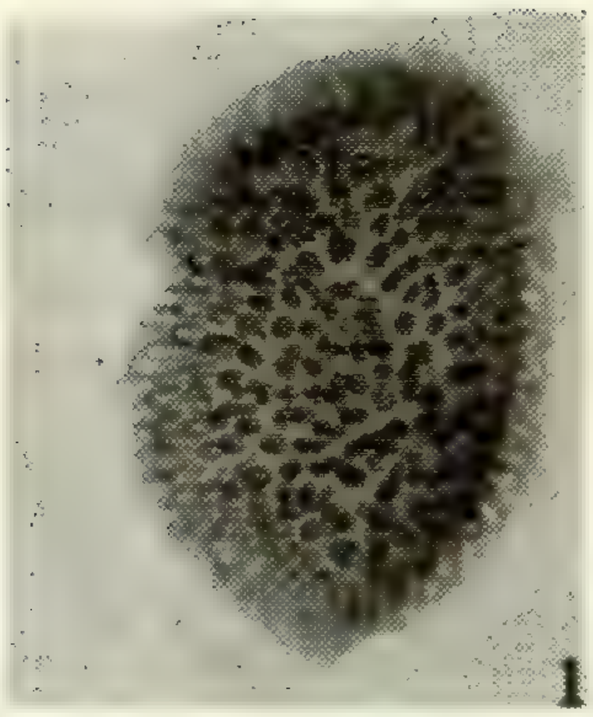
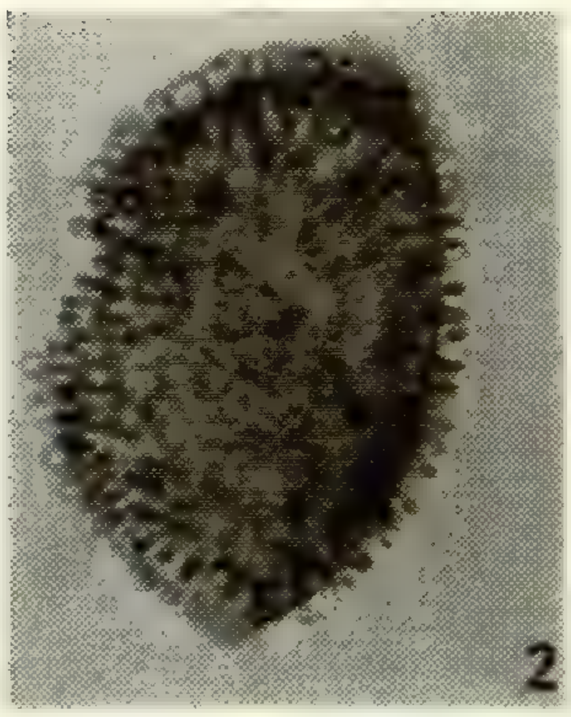
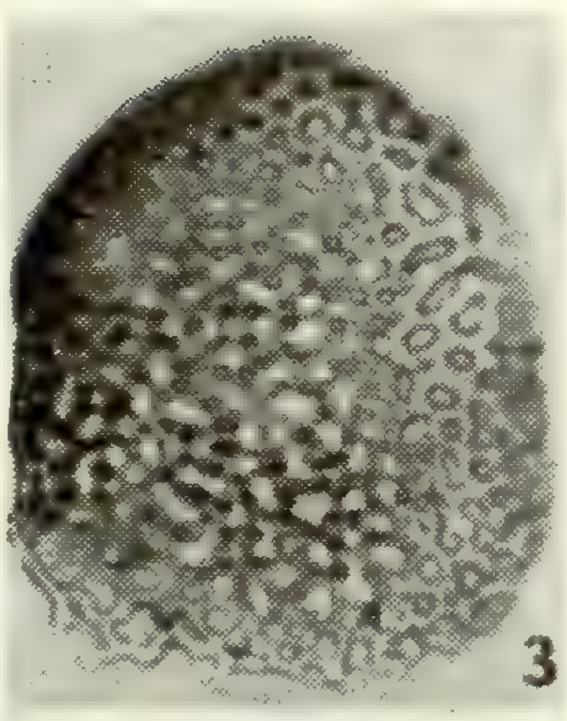
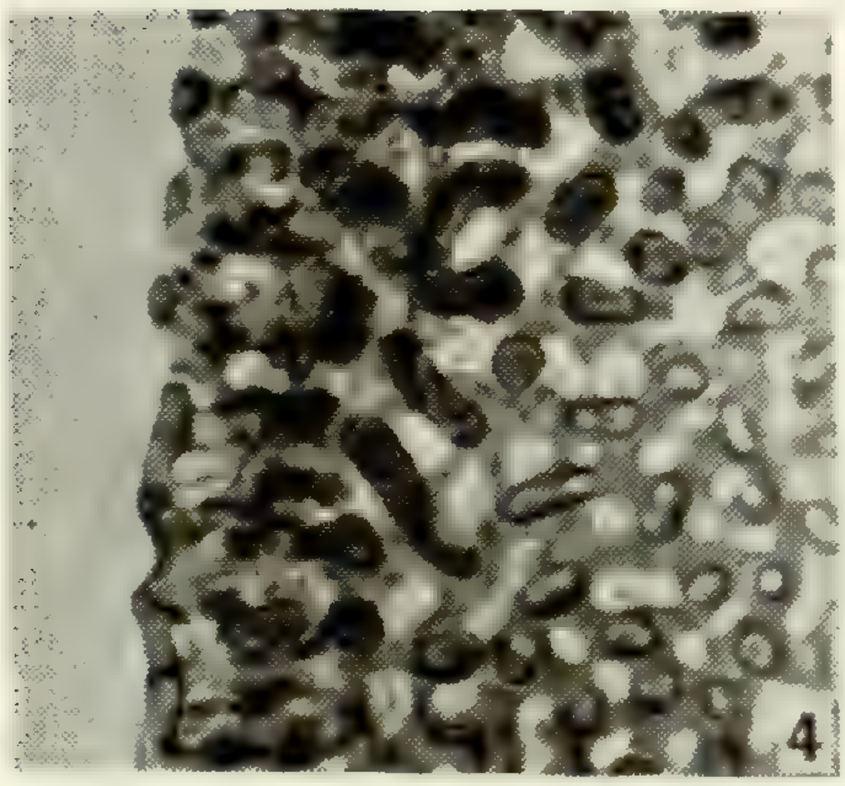


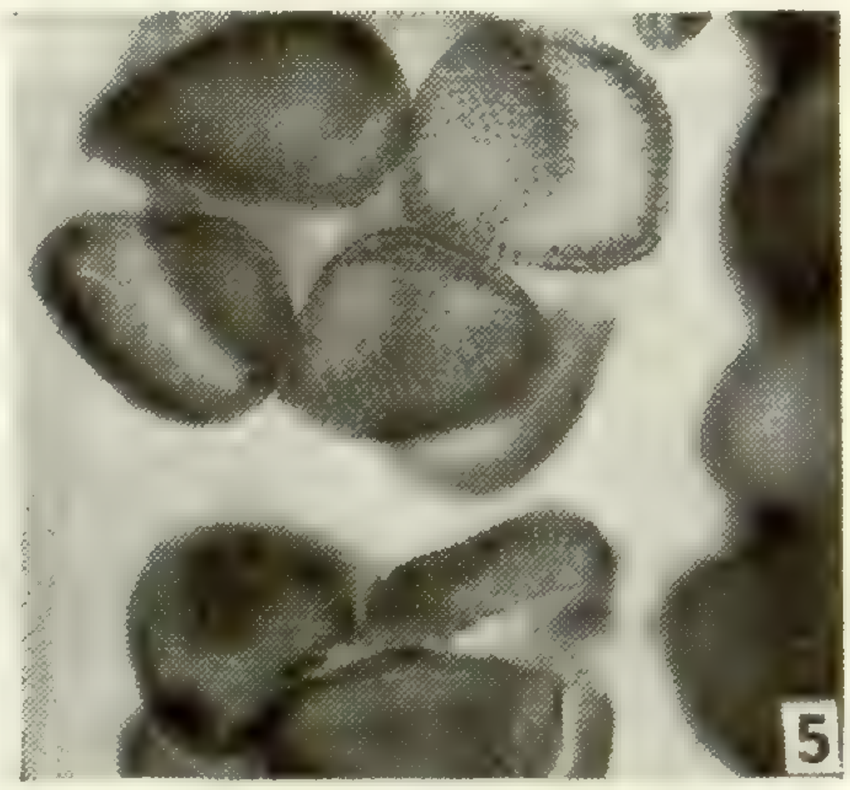
PLATE 51. FIG. 1. *Trigynaea oblongifolia* Schlecht., × 500. FIG. 2–4. *Disepalum anomalum* Hk.f., × 1000. FIG. 5. *D. platypetalum* Merr., × 200. FIG. 6. *D.* sp. (=*Polyalthia plagioneura* Diels), × 200.

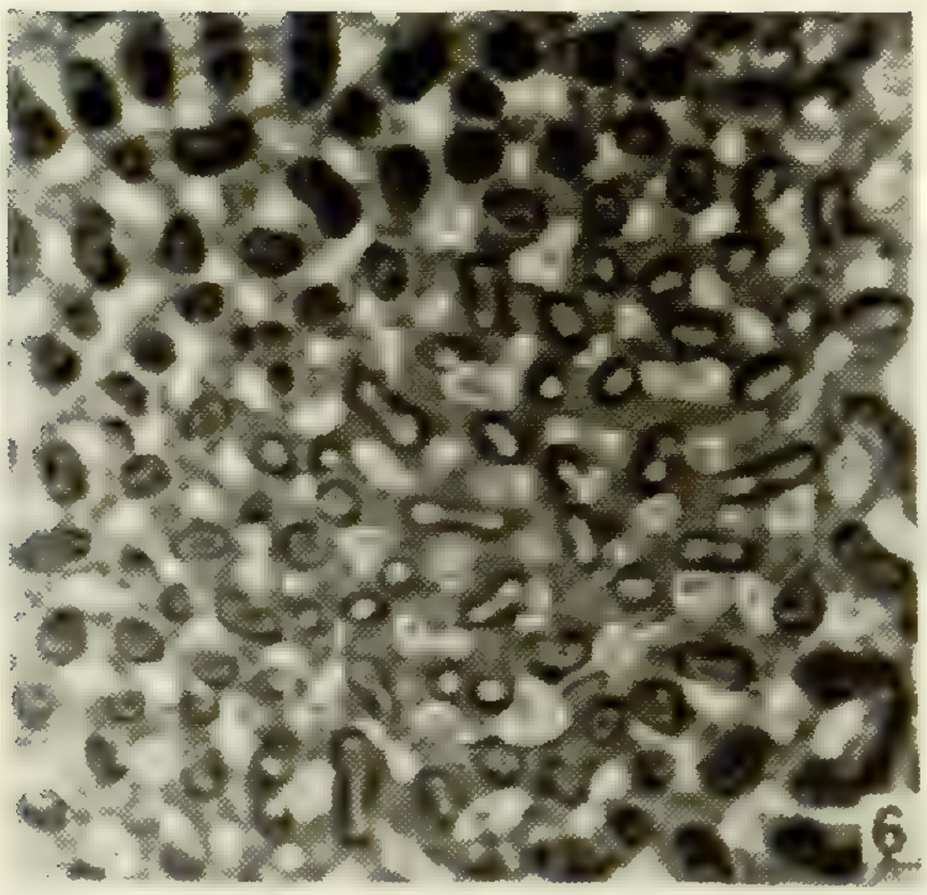












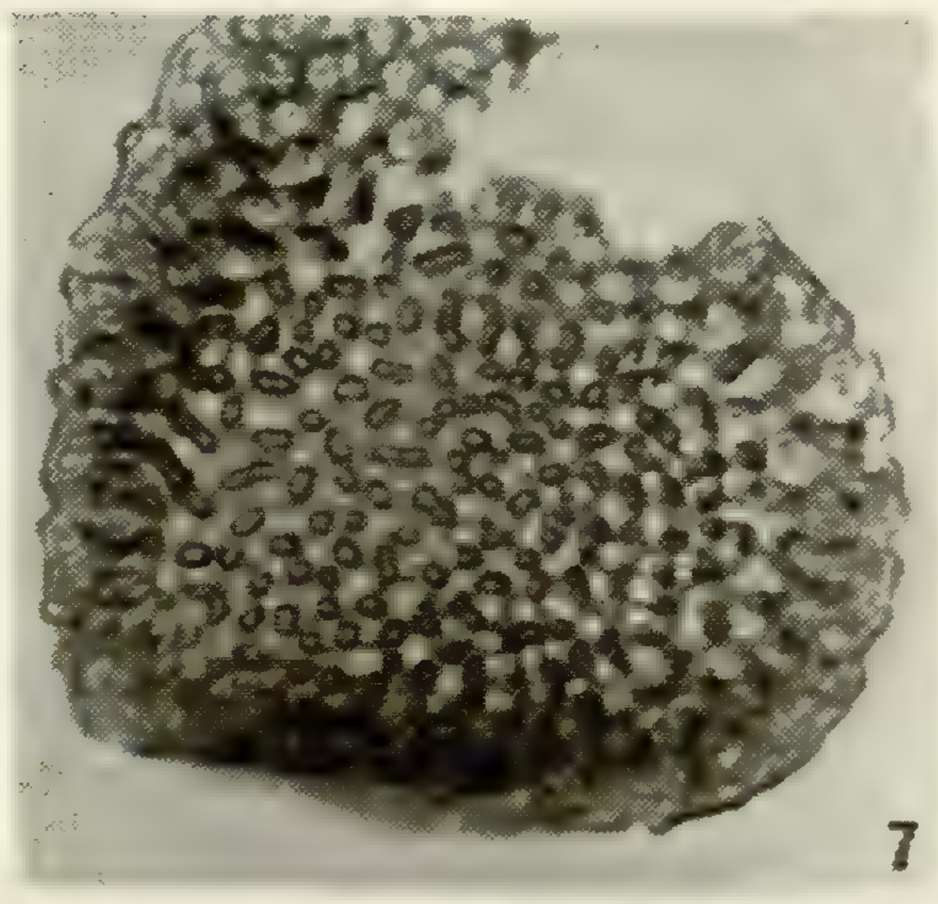
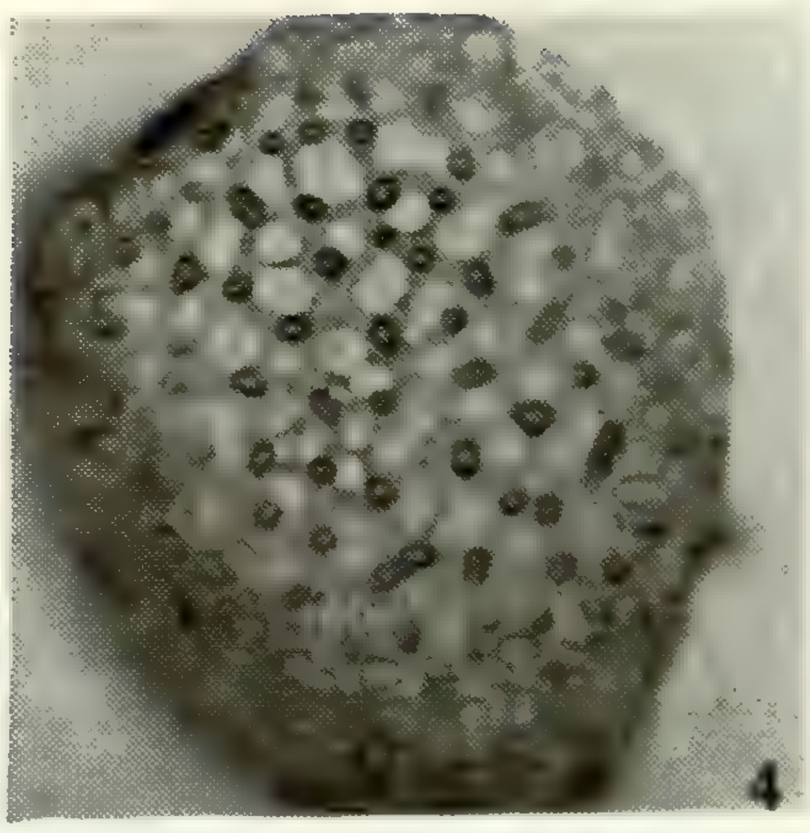
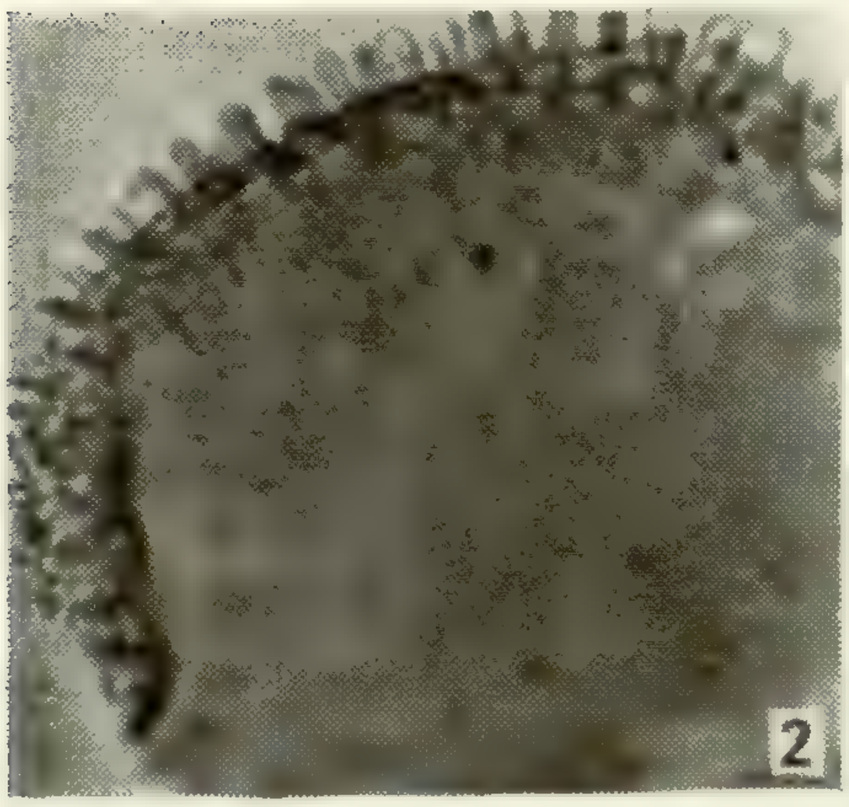
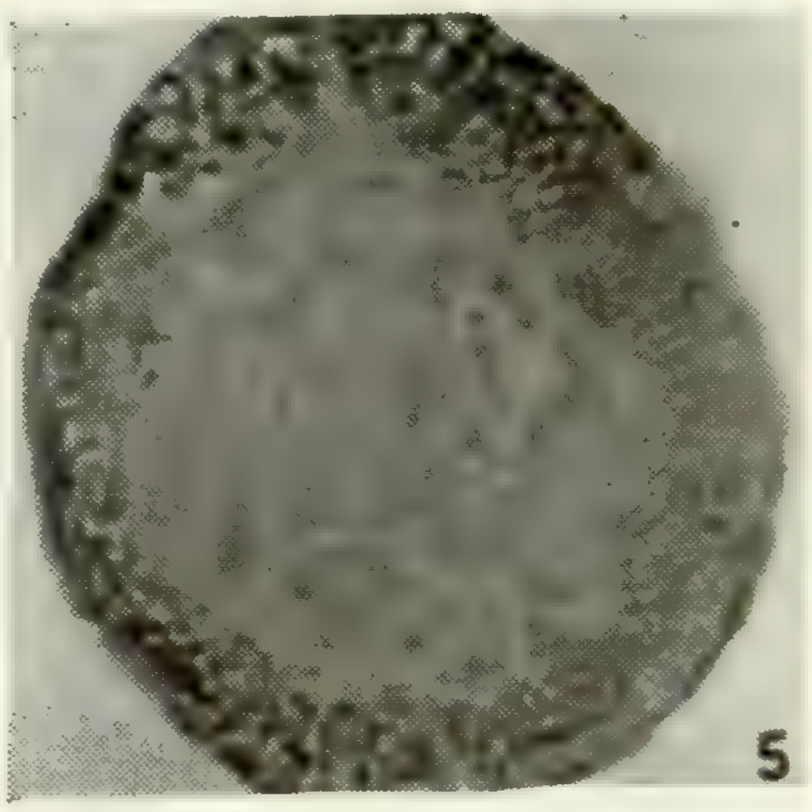
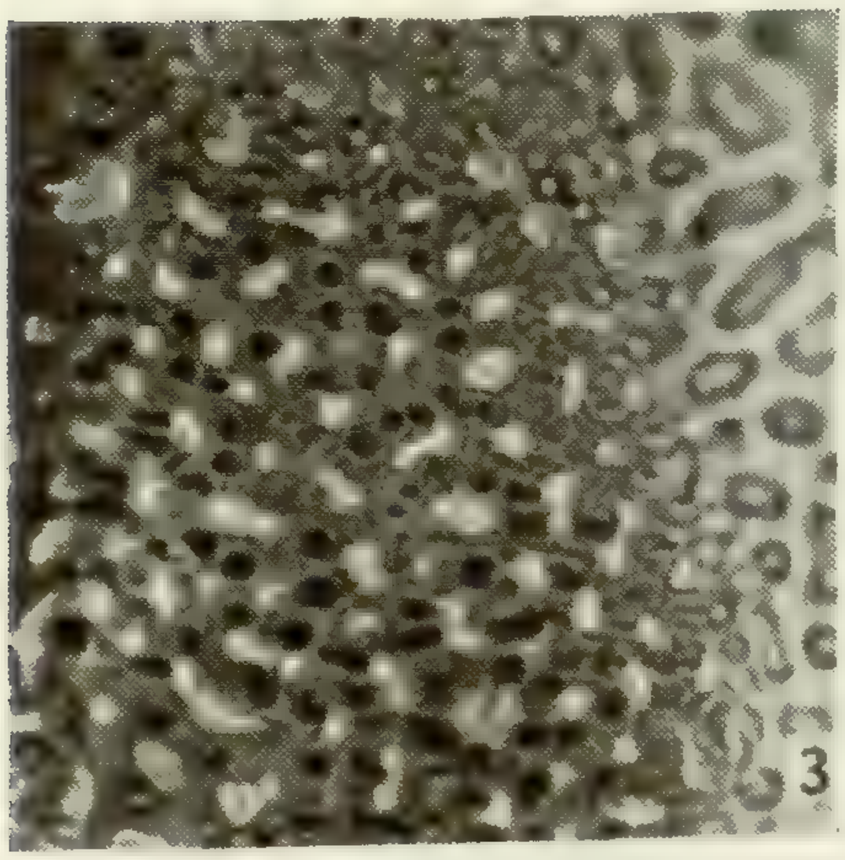


PLATE 52. FIG. 1,2. *Trigynaea ecuadorensis* R. E. Fries, × 500. FIG. 3. *Hornschuchia bryotrophe* Nees, × 500. FIG. 4. *Disepalum* sp. (=*Polyalthia plagioneura* Diels), × 1000. FIG. 5. *D.* sp. (=*Polyalthia petelotii* MERR.), × 200. FIG. 6,7. *D.* sp. (=*Polyalthia plagioneura* Diels); Fig. 6, × 1000; Fig. 7, × 500.









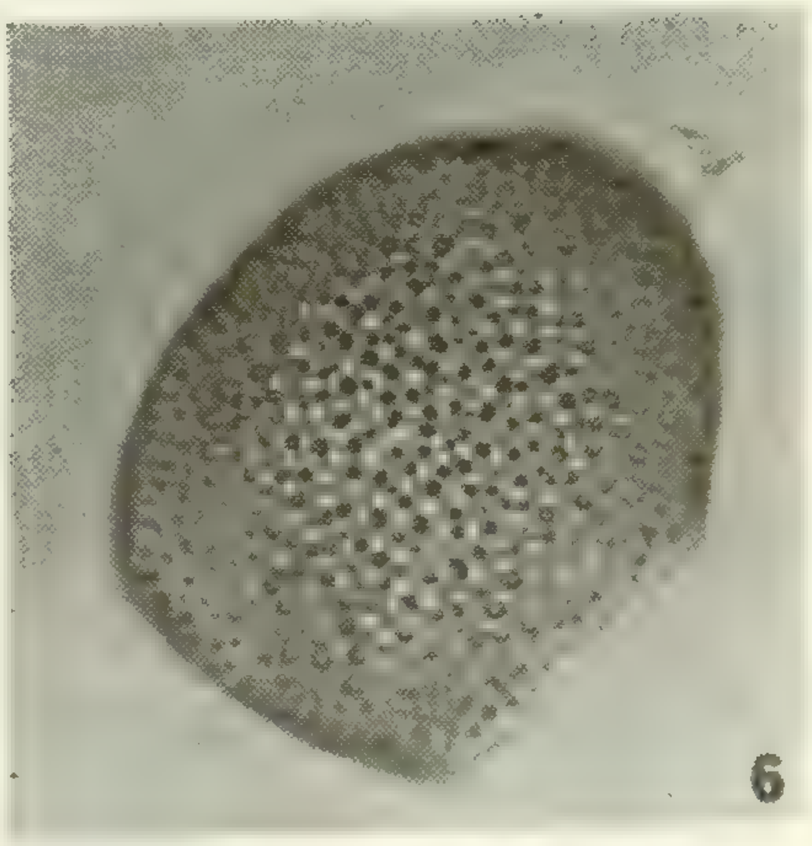
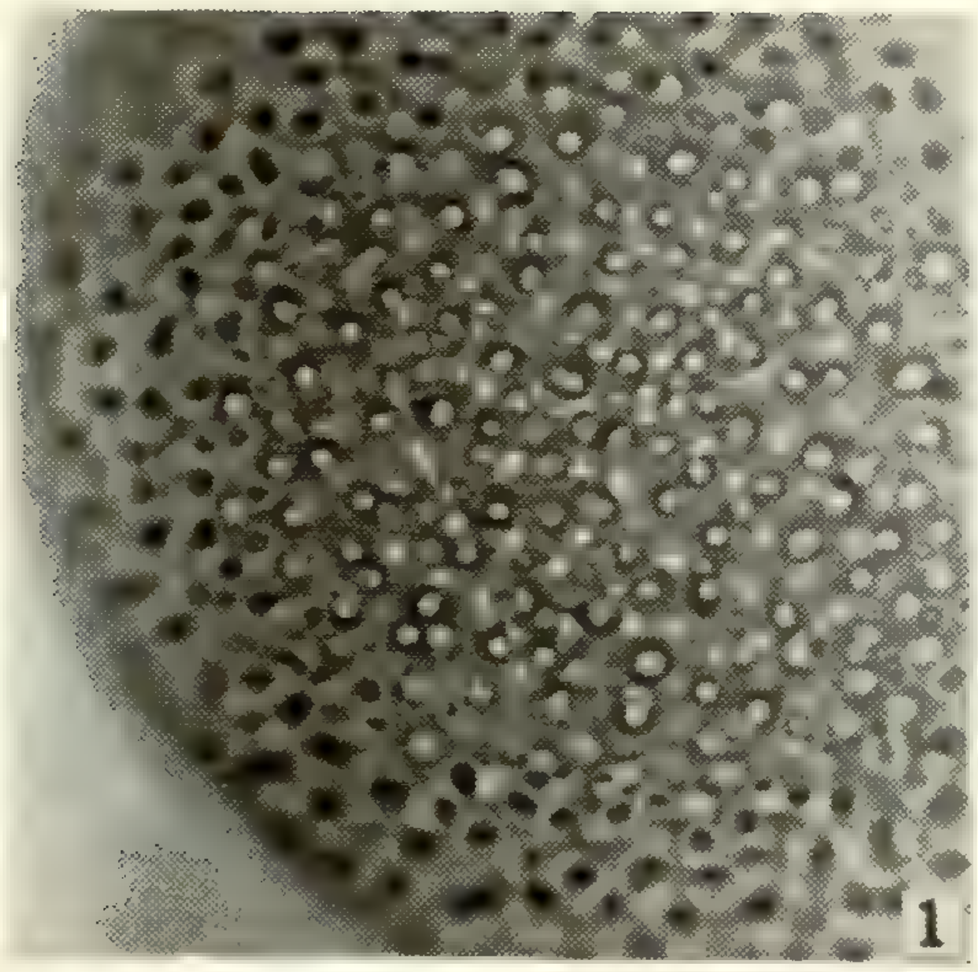
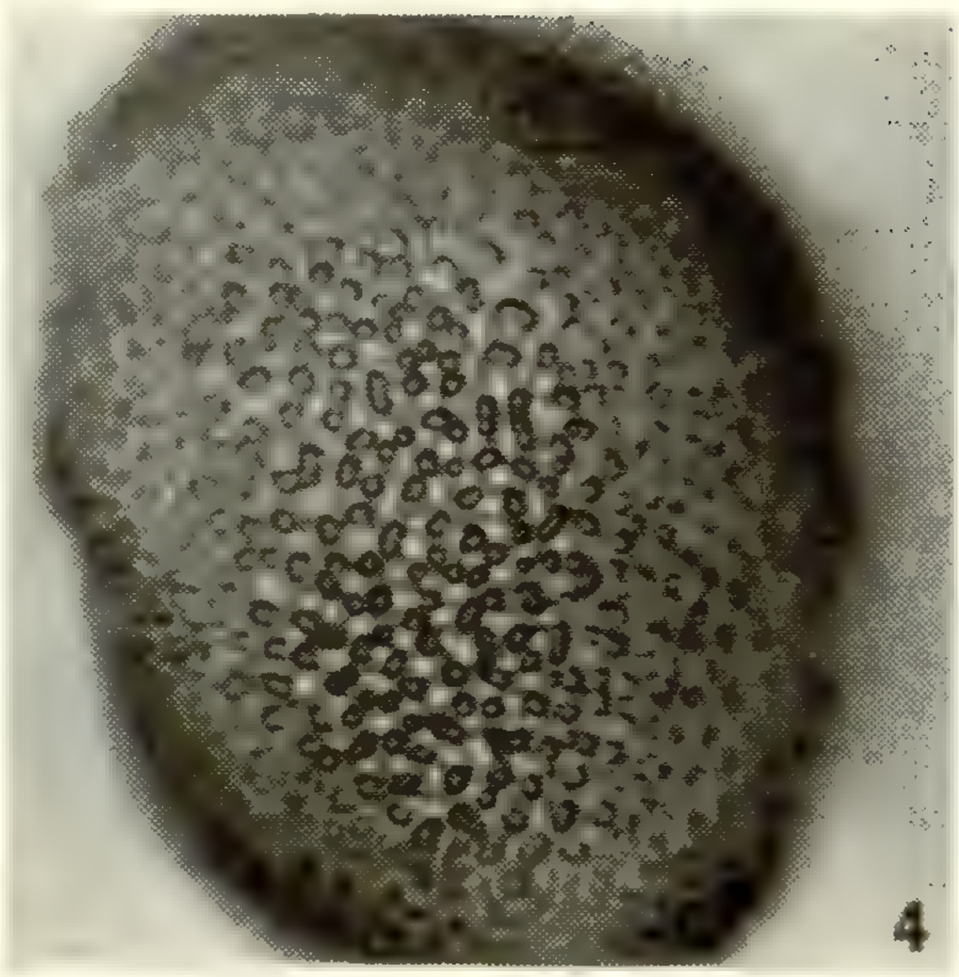
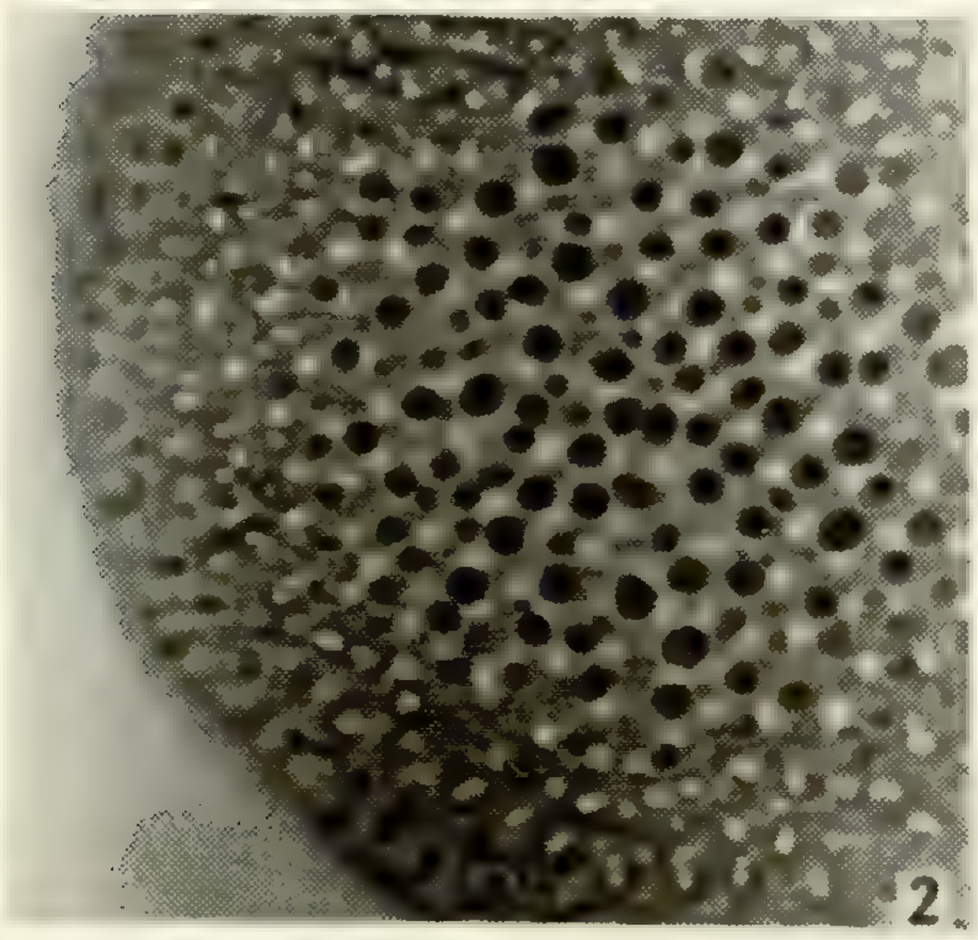
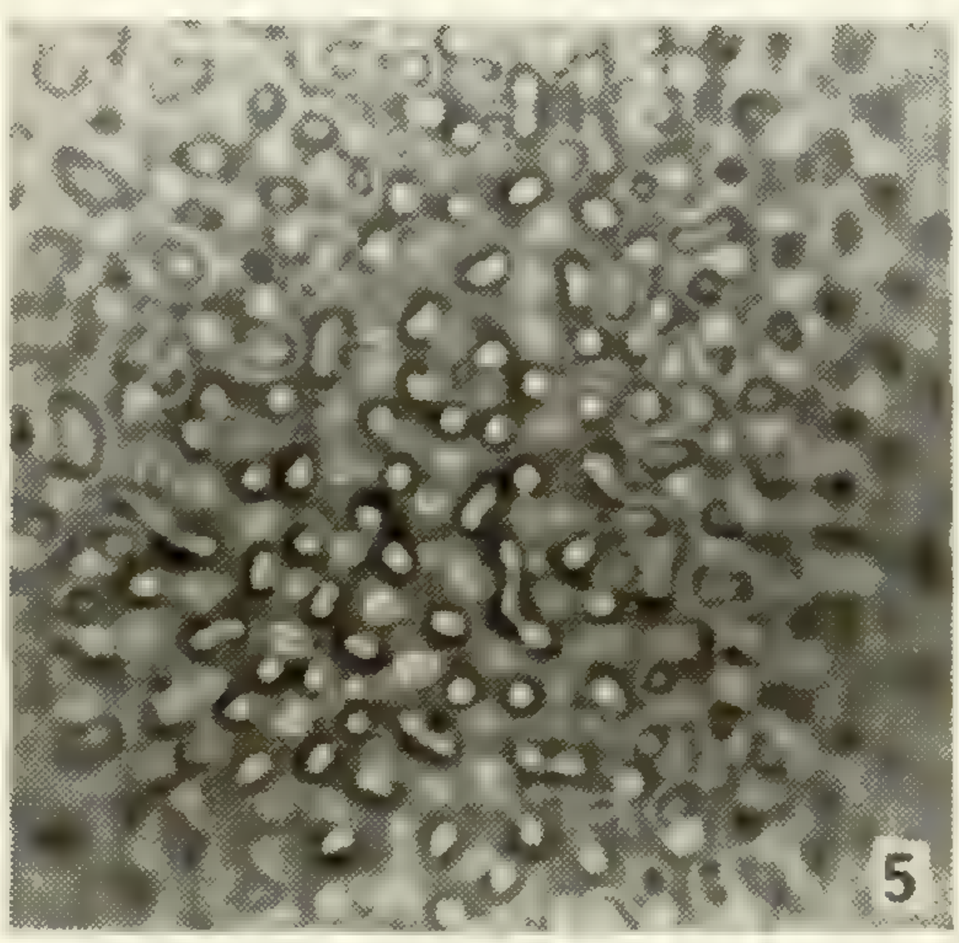


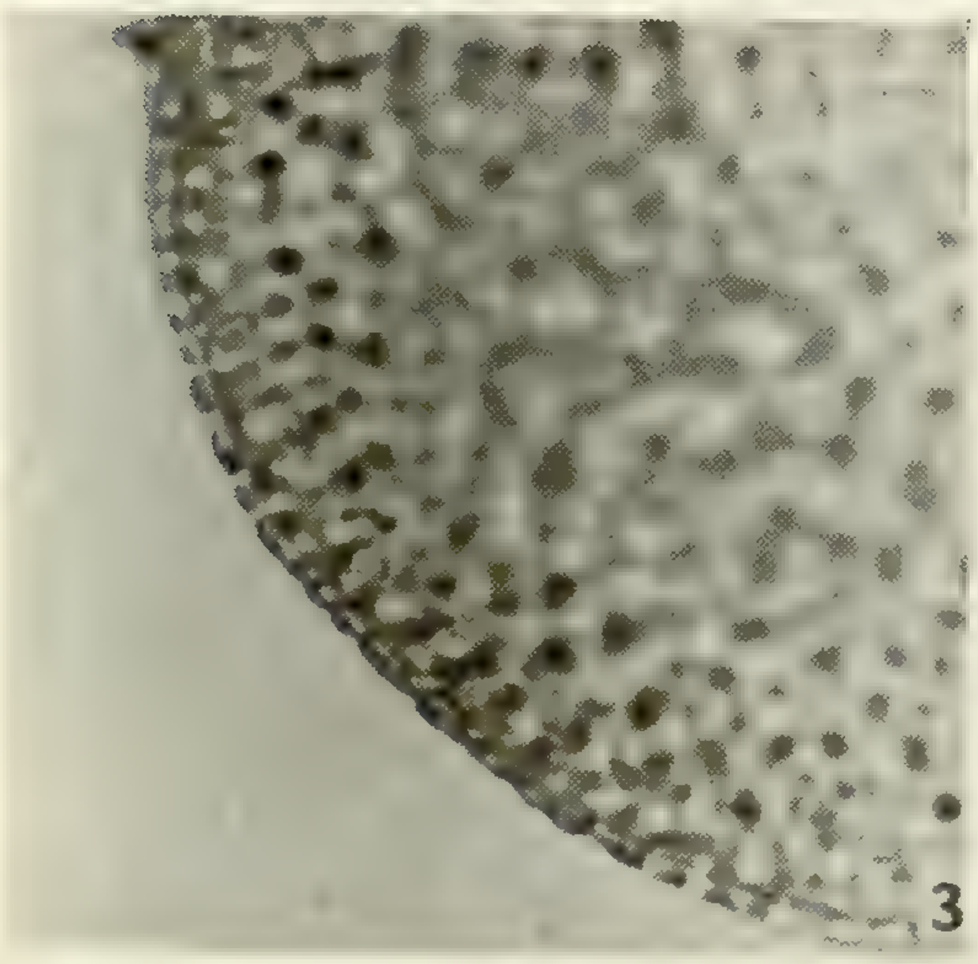
PLATE 53. FIG. 1,2. *Trigynaea caudata* (R. E. Fries) R. E. Fries, × 1000. FIG. 3. *Hornschuchia bryotrophe* Nees, × 1000. FIG. 4,5. *Disepalum anomalum* Hk.f., × 500. FIG. 6. *D. coronatum* Becc., × 500.











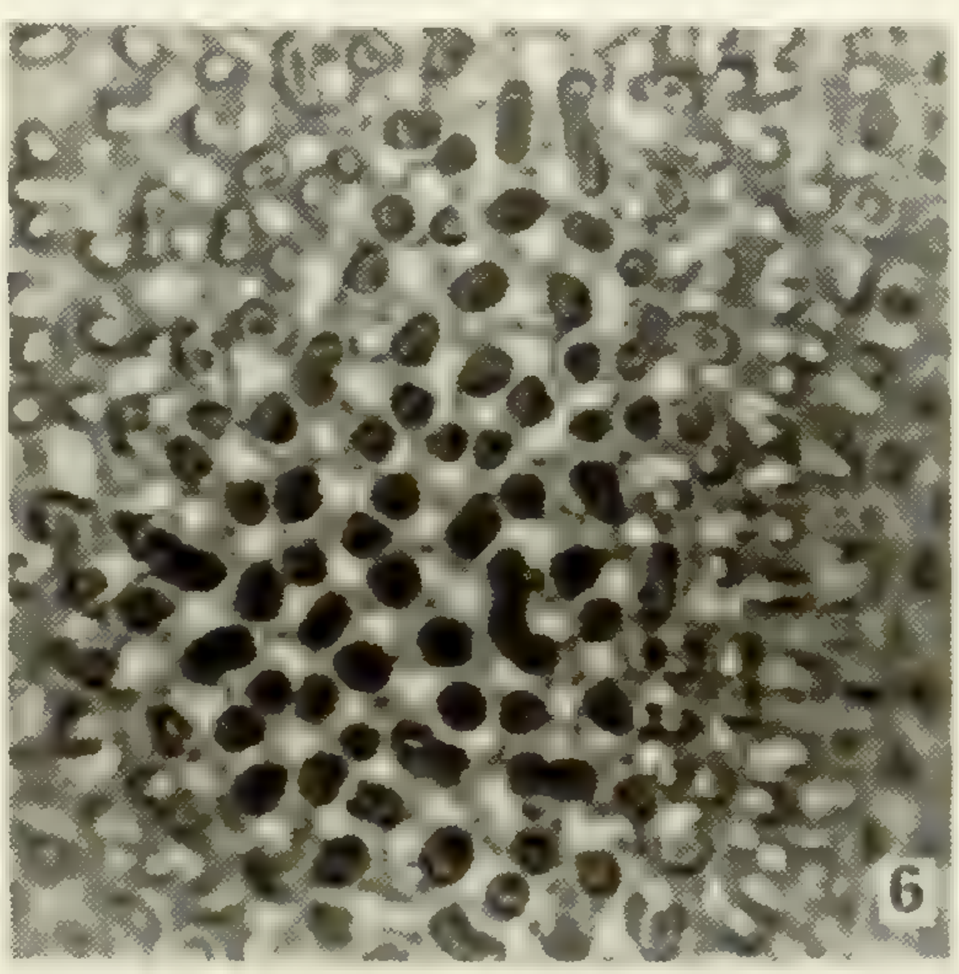


PLATE 54. FIG. 1–3. *Disepalum coronatum* Becc., × 1000. FIG. 4–6. *D.* sp. (=*Polyalthia petelotii* Merr.); Fig. 4, × 500; Fig. 5,6, × 1000.

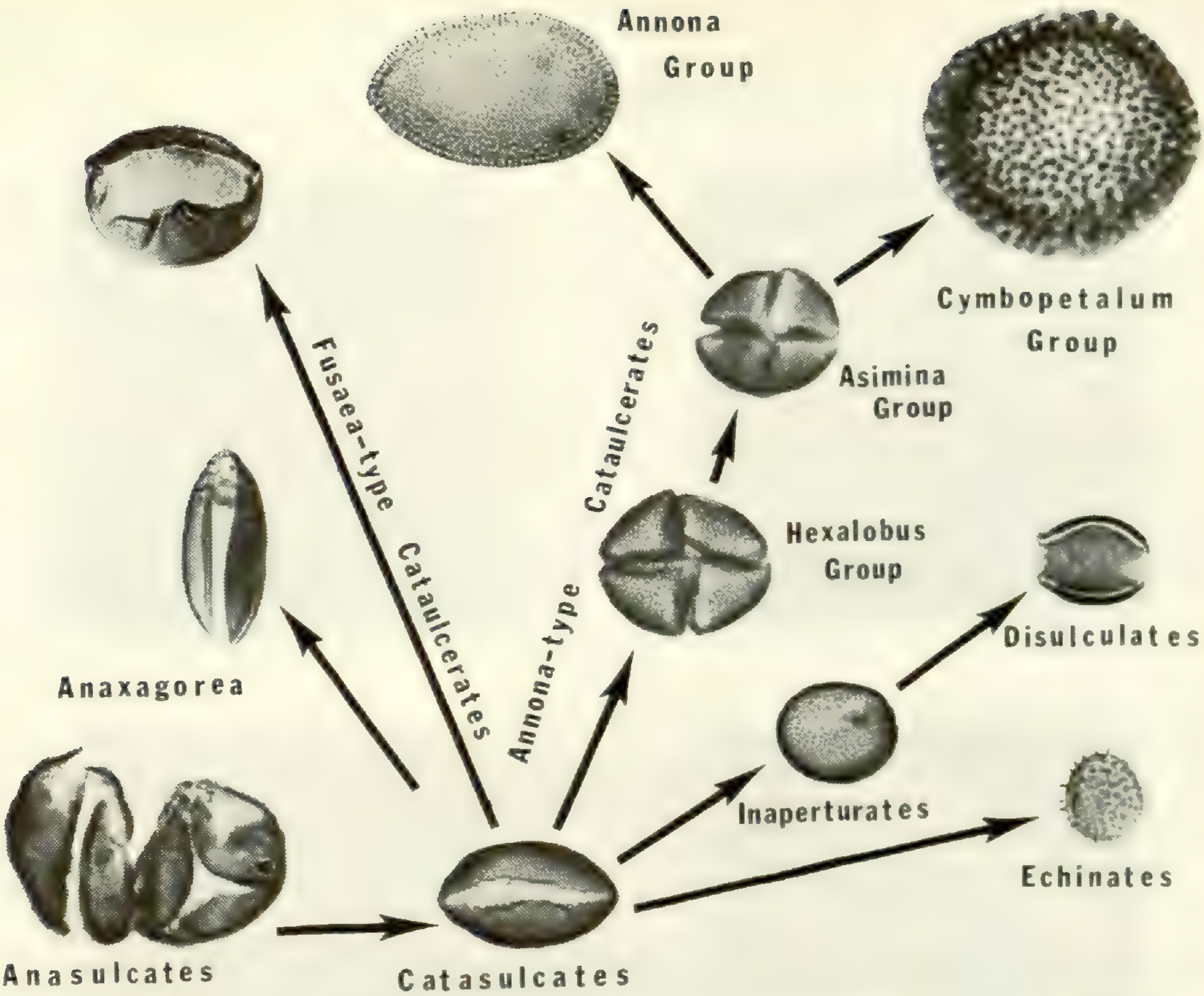


PLATE 55. POLLEN TRENDS IN THE ANNONACEAE

Anasulcates—*Pseudoxandra coriacea.* Catasulcates—*Cremastosperma megalophyllum.* Echinates—*Desmos dunalii.* Inaperturates—*Papualthia reticulata.* Disulculates—*Sapranthus* sp., Anaxagorea—*Anaxagorea dolichocarpa.* Fusea-type cataulcerates—*Goniothalamus saigonensis.* Hexalobus group—*Hexalobus monopetalus.* Asimina group—*Asimina triloba.* Annona group—*Annona muricata.* Cymbopetalum group—*Cymbopetalum odoratissimum.* (All magnifications the same except for the grains of *Asimina, Annona, and Cymbopetalum,* which are reduced by about one-half relative to the other grains.)

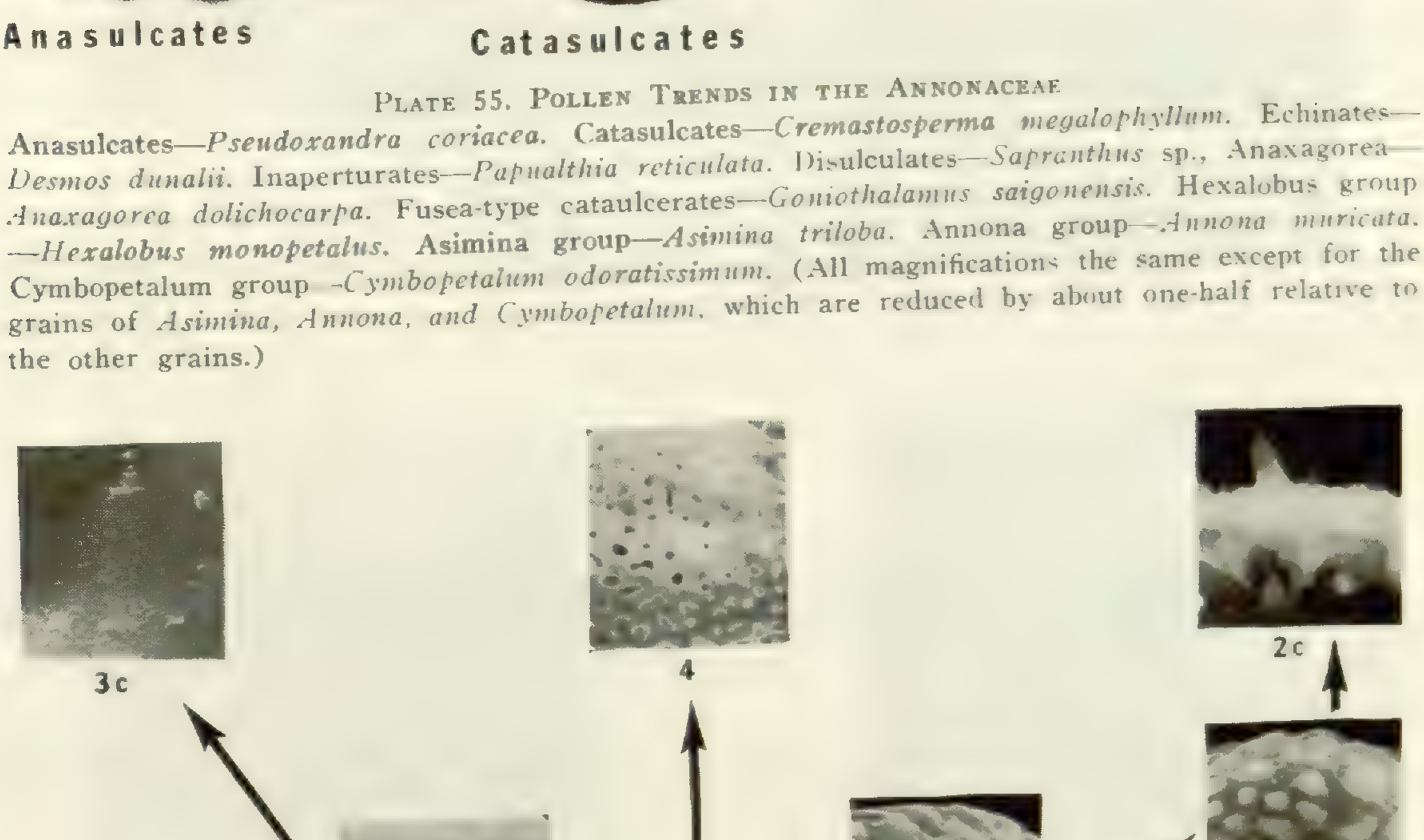
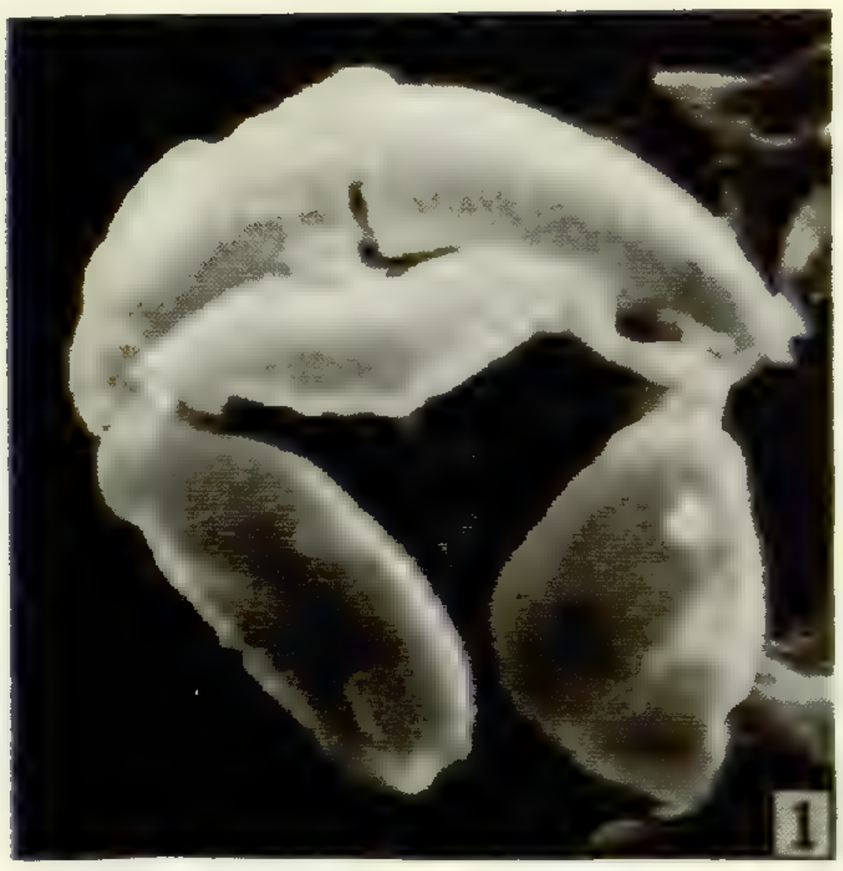
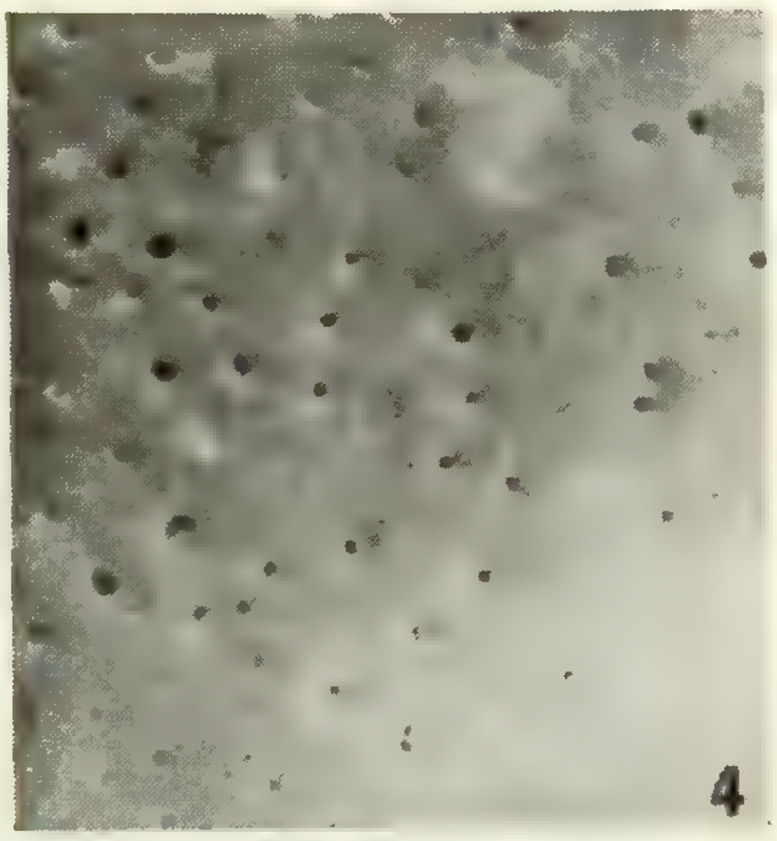


PLATE 56. POLLEN SCULPTURING TRENDS IN THE ANNONACEAE

1a. *Malmea costaricensis.* 1b. *Polyalthia glauca.* 2a. *Reedrollinsia* Walker. 2b. *Orophea luzonensis.* 2c. *Dasymaschalon sootepense.* 3a. *Pseudoxandra coriacea.* 3b. *Cananga odorata.* 3c. *Fusaea longifolia.* 4. *Cymbopetalum odoratissimum.* (All photographs are scanning electronmicrographs.)





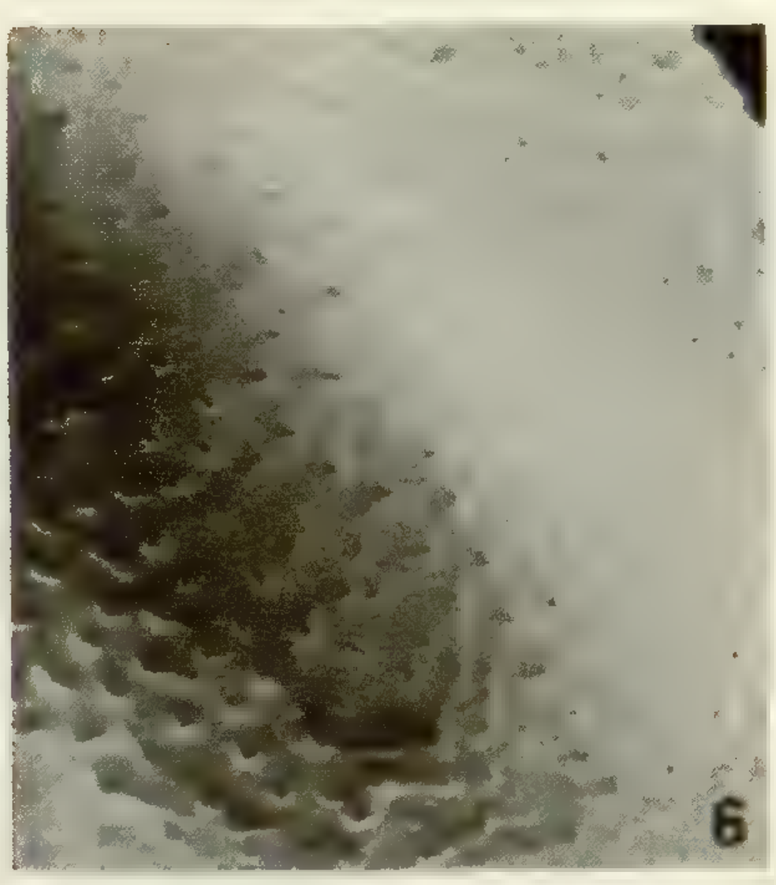
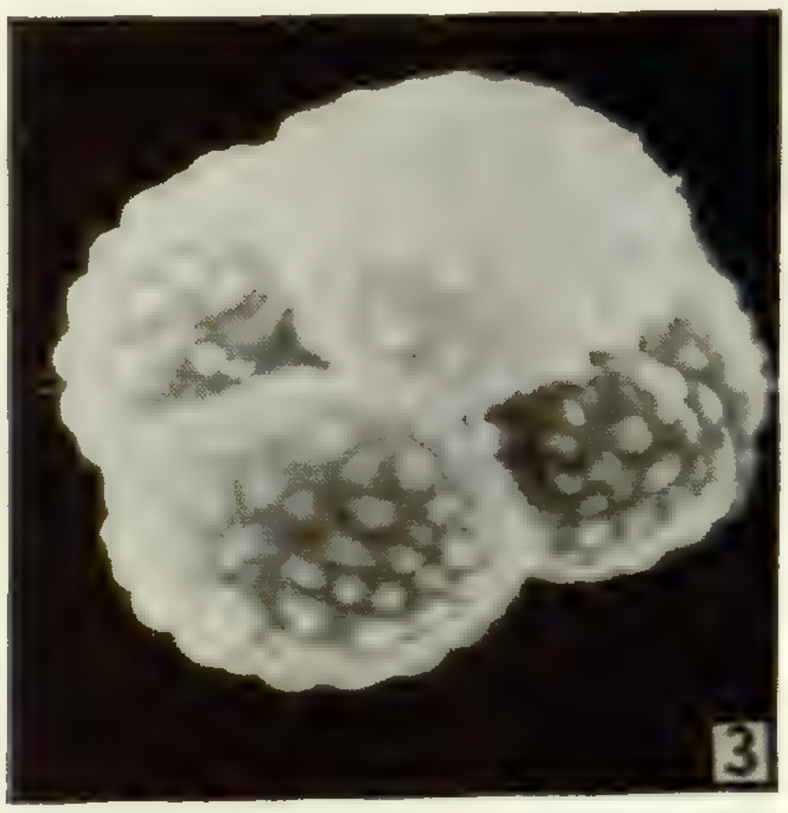


PLATE 57. FIG. 1,2. *Pseudoxandra coriacea* R. E. Fries; Fig. 1, × ca. 490; Fig. 2, × ca. 4100. FIG. 3,4. *Malmea costaricensis* R. E. Fries; Fig. 3, × ca. 490; Fig. 4, × ca. 1850. FIG. 5,6. *Polyalthia glauca* (Hassk.) Boerl.; Fig. 5, × ca. 700; Fig. 6, × ca. 2100. (All photographs are scanning electronmicrographs.)



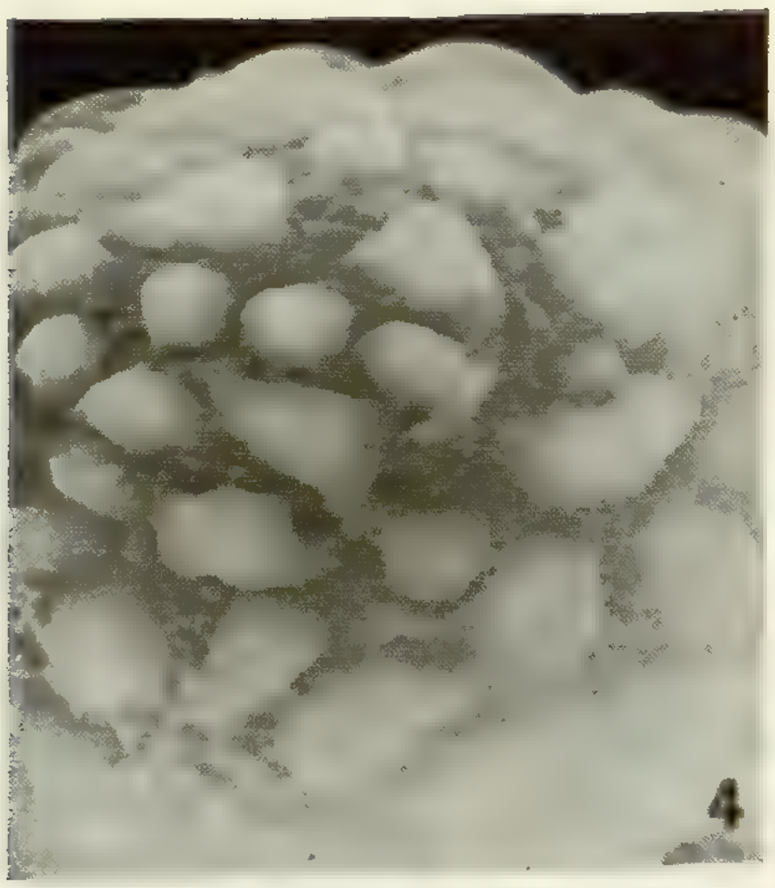
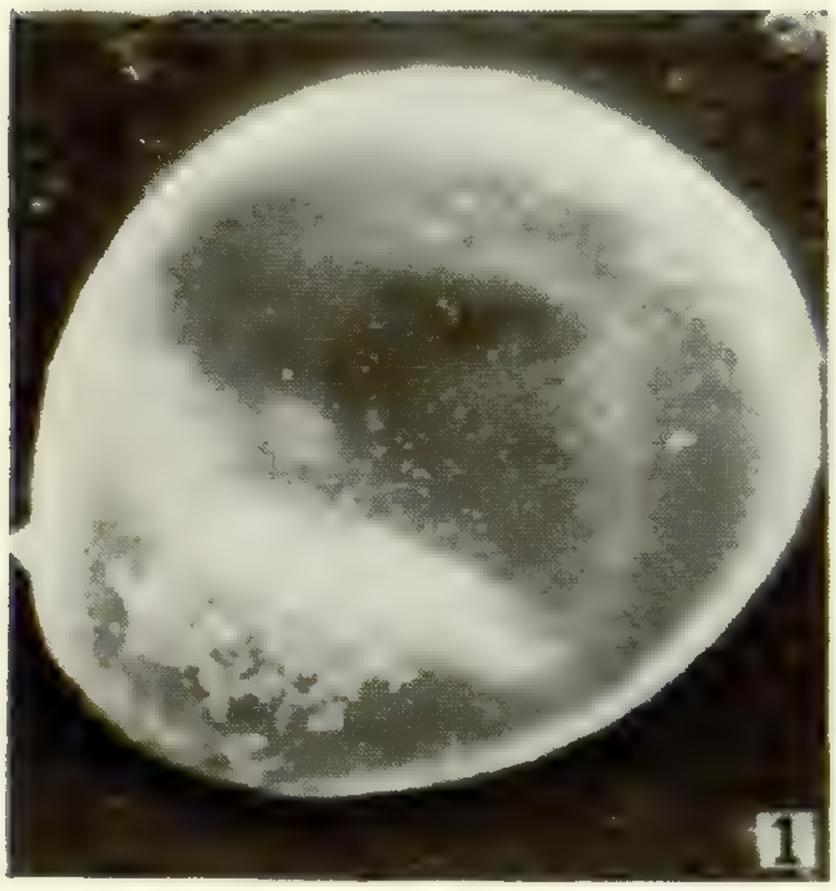
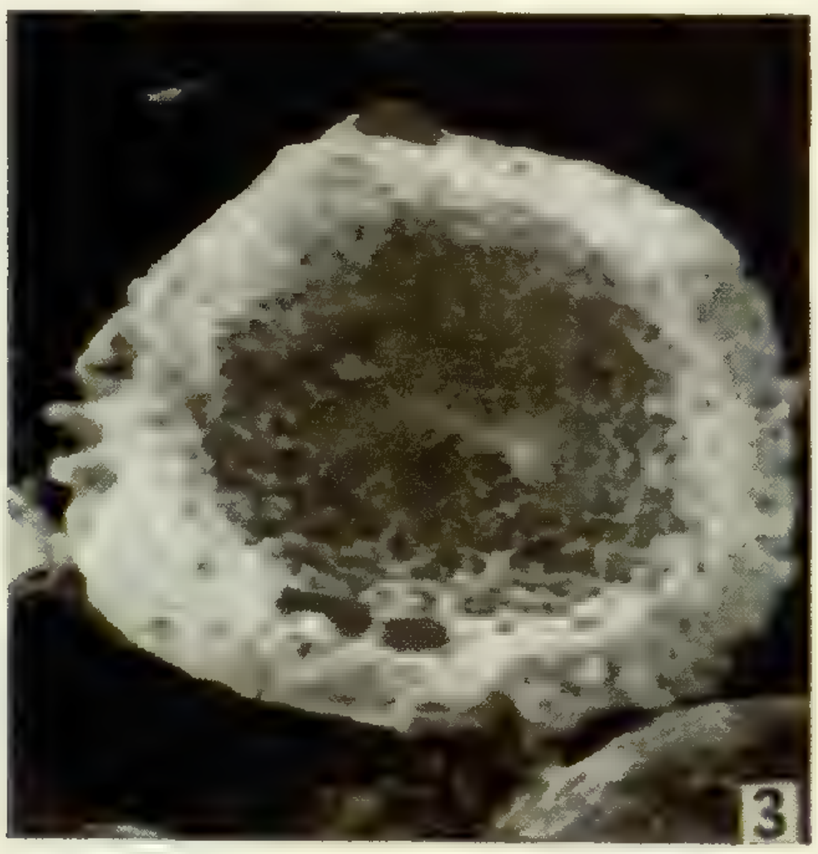
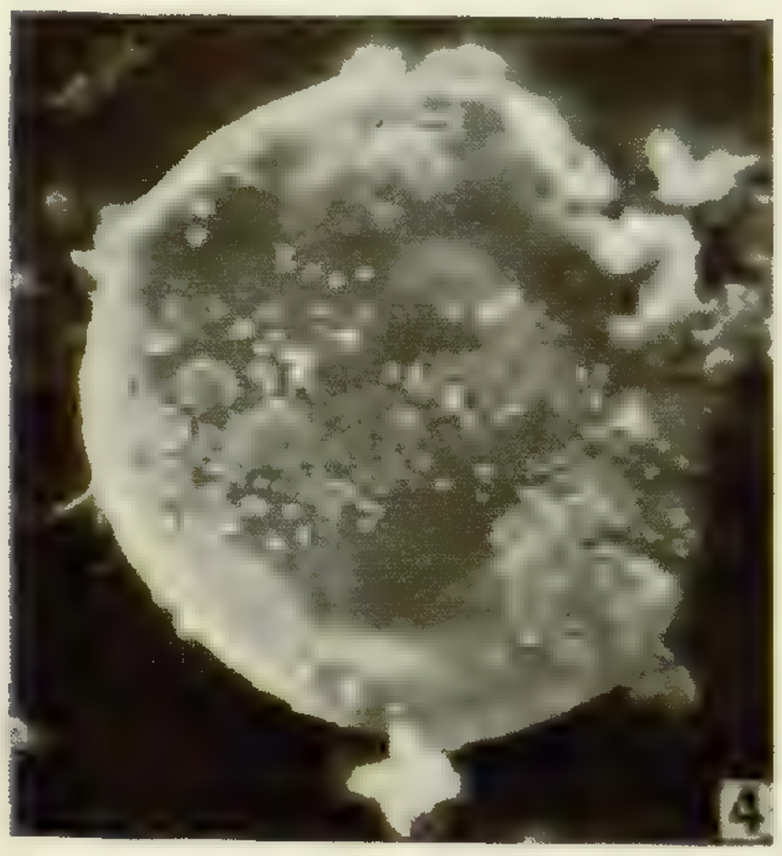


PLATE 58. FIG. 1,2. *Dasymaschalon sootepense* Craib; Fig. 1, × ca. 760; Fig. 2, × ca. 2660. FIG. 3–5. *Orophea luzonensis* Merr.; Fig. 3, × ca. 480; Fig. 4, × ca. 1370; Fig. 5, × ca. 3400. (All photographs are scanning electronmicrographs.)







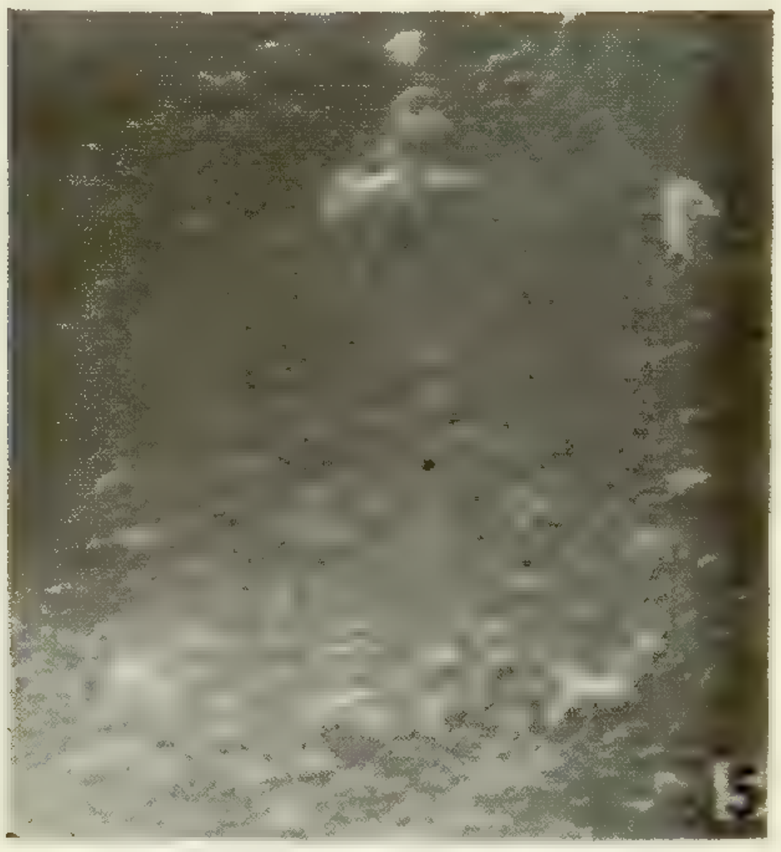
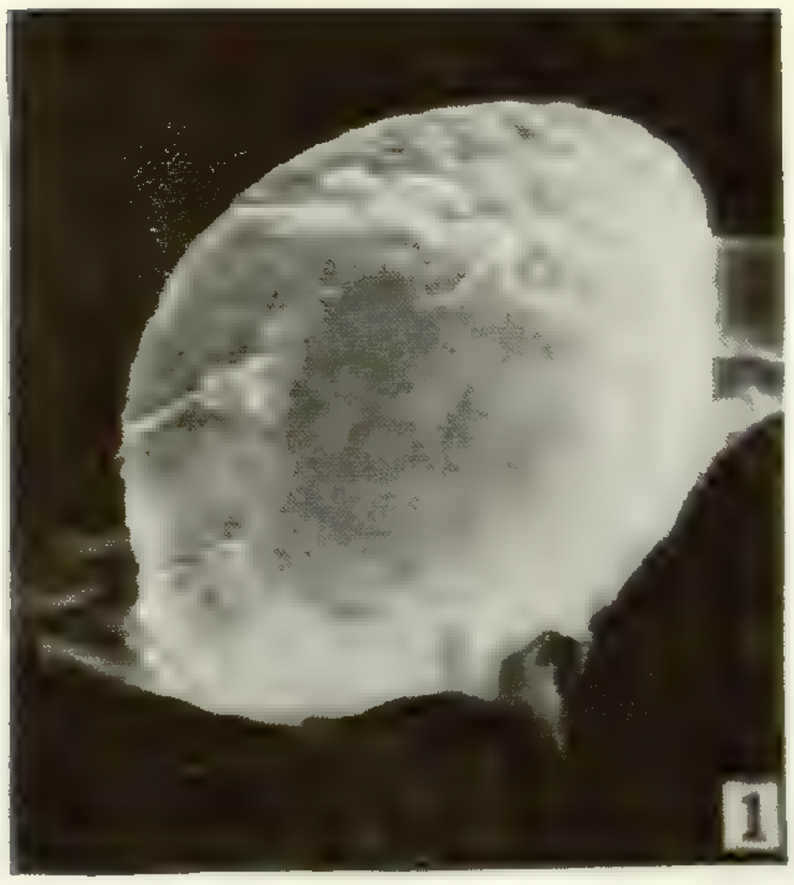
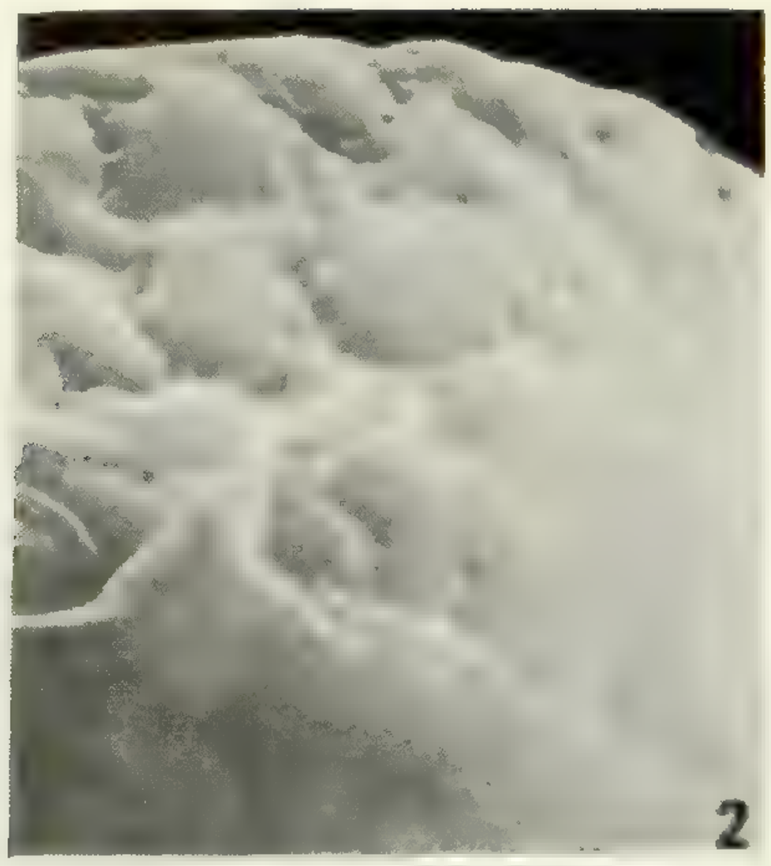


PLATE 59. FIG. 1,2. *Cananga odorata* (Lam.) Hk.f. & Th.; Fig. 1, × ca. 400; Fig. 2, × ca. 3200. FIG. 3. *Cymbopetalum odoratissimum* Barb. Rodr., × ca. 135. FIG. 4,5. ***Fusaea longifolia*** **(Aubl.) Saff.; Fig. 4, × ca. 280; Fig. 5,** × ca. 2800. (All photographs are scanning electronmicrographs.)





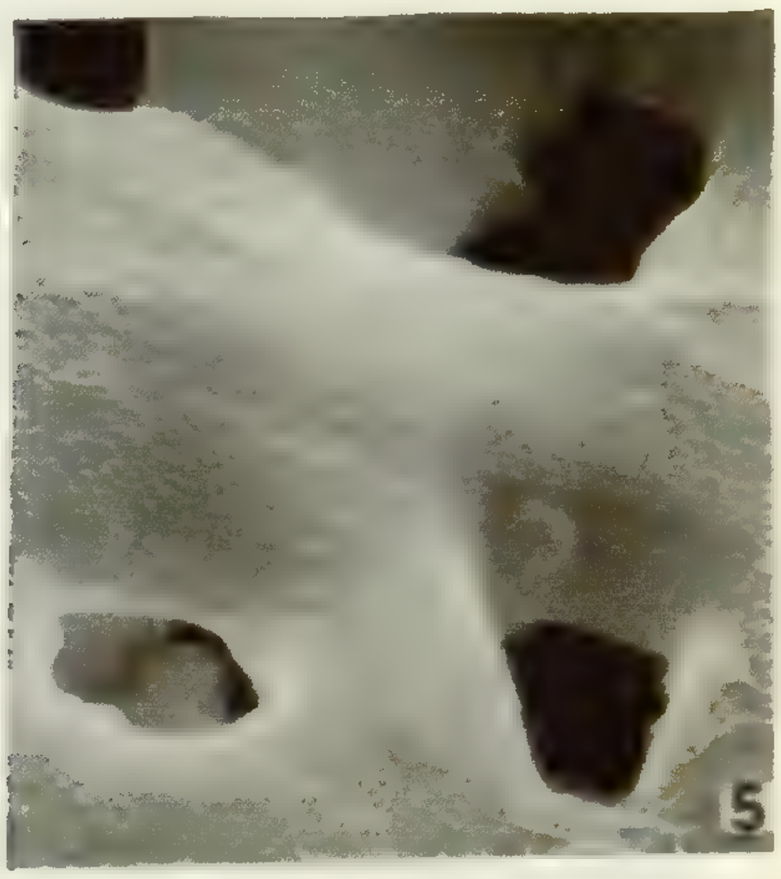
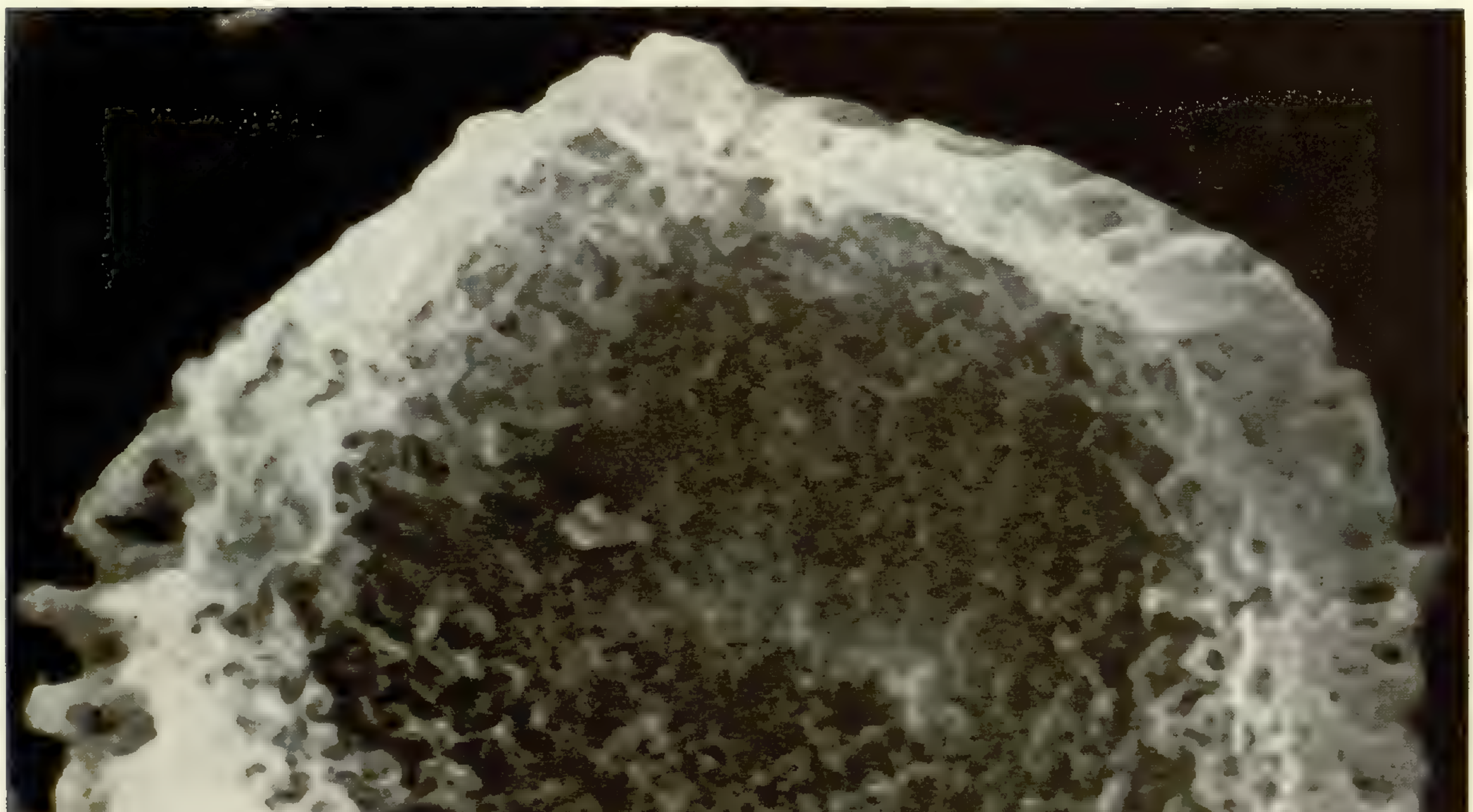


PLATE 60. FIG. 1,2. *Reedrollinsia* Walker; **Fig. 1, × ca. 760; Fig. 2, × ca. 2280.** FIG. 3–5. *Cymbopetalum odoratissimum* Barb. Rodr.; **Fig. 3, × ca. 140; Fig. 4, × ca. 350; Fig. 5, × ca. 2100. (All photographs are scanning electronmicrographs.)**



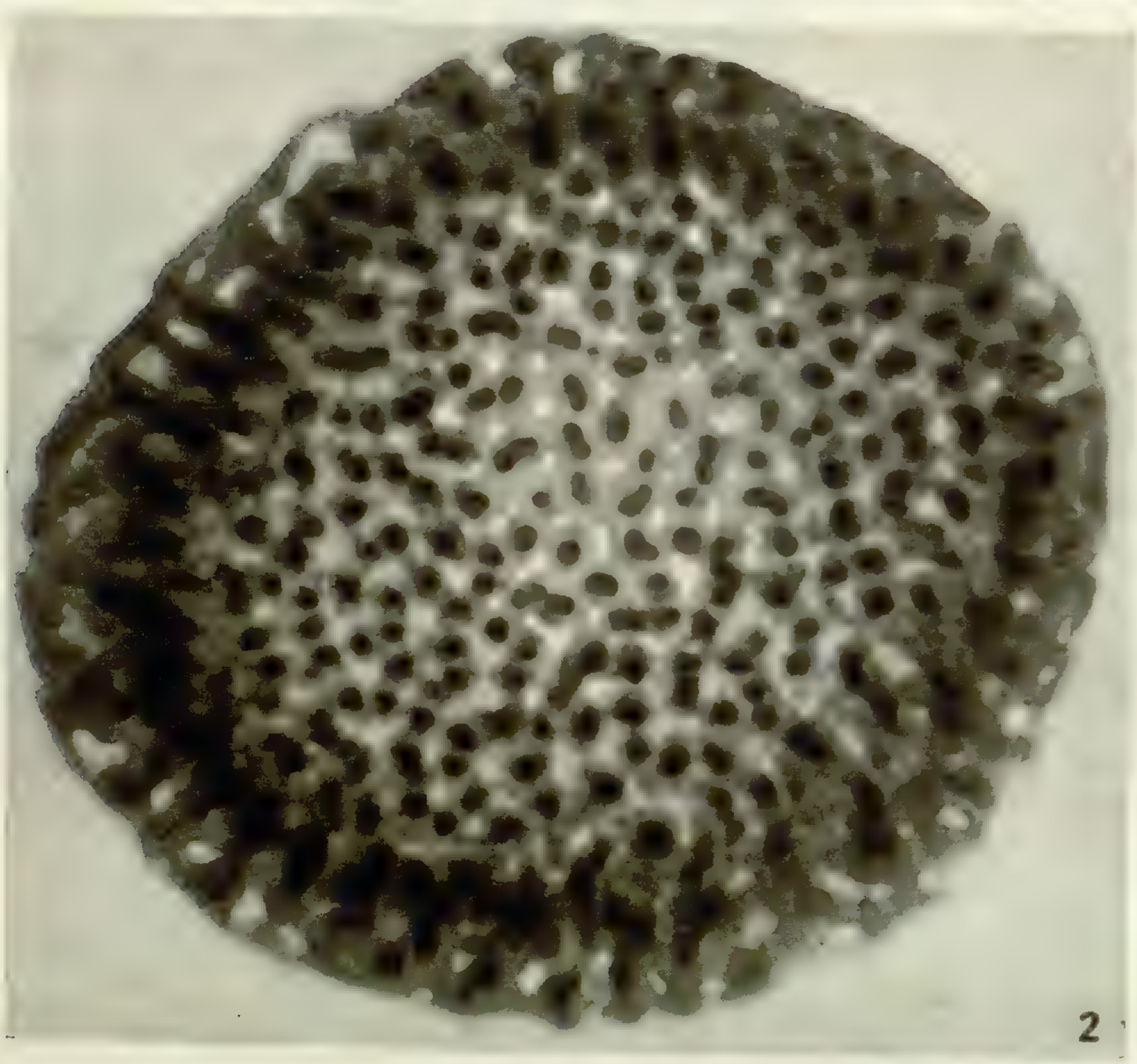


PLATE 61. *Cymbopetalum odoratissimum* Barb. Rodr. This species probably has the largest fixiform pollen grain in the angiosperms, with some grains as large as 350μ. FIG. 1. Scanning electronmicrograph of the proximal face. × ca. 360. FIG. 2. Photomicrograph of the distal face, × ca. 320.

APPENDIX: CITATION OF VOUCHER SPECIMENS

Pseudoxandra *coriacea* R. E. Fries (dupl. det. R. E. Fries, 1959), J. J. Wurdack & L. S. Adderley 43492–NY, P–579*; *P. guianensis* (R. E. Fries) R. E. Fries (det. L. Aristeguieta, 1967), Felix Cardona 1642–NY, P–580; *P. leiophylla* (Diels) R. E. Fries, R. Spruce 2473 (isotype)-GH, P–187; *P. polyphleba* (Diels) R. E. Fries (det. L. Aristeguieta, 1967), B. A. Krukoff 4882–NY, P–581; *P. williamsii* (R. E. Fries) R. E. Fries (det. R. E. Fries, 1933–as *Cremastosperma*), Llewelyn Williams 3960 (type)-F, P–656.

Cremastosperma *anomalum* R. E. Fries, W. L. Stern et al. 107–GH, P–160; *C. cauliflorum* R. E. Fries (det. R. E. Fries/cit. Arkiv), J. Cuatrecasas 11125–NY, P–547; *C. gracilipes* R. E. Fries, Llewelyn Williams 5296–F, P–653; *C. leiophyllum* (Diels) R. E. Fries (det. R. E. Fries, 1947), E. P. Killip & A. C. Smith 23004–US, P–611; *C. longicuspe* R. E. Fries (det. R E. Fries, 1937), Llewelyn Williams 4092–F, P–654; *C. megalophyllum* R. E. Fries, G. Klug 3069–GH, P–111; *C. microcarpum* R. E. Fries (det. L. Aristeguieta, 1967), G. T. Prance et al. 3527–NY, P–548; *C. novogranatense* R. E. Fries (det. L. Aristeguieta, 1967), J. Cuatrecasas & L. Willard 26031–US, P–612; *C. pedunculatum* (Diels) R. E. Fries, G. Klug 3726–A & GH, P–112.

Malmea *costaricensis* R. E. Fries, Walker 395†; *M. depressa* (Baill.) R. E. Fries, G. F. Gaumer & Sons 23903–GH, P–105; *M. diclina* R. E. Fries (det. R. E. Fries, 1956), Richard Evans Schultes & George A. Black 8534–US, P–615; *M. discolor* R. E. Fries (det. L. Aristeguieta, 1967), Forest Dept. Brit. Guiana 3589–NY, P–565; *M. hypoglauca* (Standl.) R. E. Fries, H. Pittier 4337–US, P–614; *M. obovata* R. E. Fries, Riedal (no number on the sheet, but probably Riedal 525, then an isotype)-A, P–107; *M. raimondii* (Diels) R. E. Fries (det. R. E. Fries, 1937), Llewelyn Williams 6226–F, P–660; *M. xanthochlora* (Diels) R. E. Fries ex desc., P. C. D. Cazalet & T. D. Pennington 7796–NY, P–566.

Ephedranthus *amazonicus* R. E. Fries (det. L. Aristeguieta, 1967), G. T. Prance et al. 4692–US, P–613; *E. guianensis* R. E. Fries (det. R. E. Fries), Forest Dept. Brit. Guiana 4788–NY, P–557.

Pseudephedranthus *fragrans* (R. E. Fries) Aristeguieta, Bassett Maguire & John J. Wurdack 34954 (isotype)-GH, P–124.

Oxandra *espintana* (Spruce ex Benth.) Baill. (det. R. E. Fries), G. Klug 4273–US, P–599; *O. euneura* Diels (det. R. E. Fries, 1937), B. A. Krukoff 8177–NY, P–570; *O. krukoffii* R. E. Fries, B. A. Krukoff 1124 (isotype)-A, P–123; *O. lanceolata* (Sw.) Baill., Bro. Leon 12012–GH, P–697; *O. laurifolia* (Sw.) A. Rich., E. L. Ekman 5924–A, P–698; *O. major* R. E. Fries, B. A. Krukoff 8497 (isotype)-A, P–122; *O. mediocris* Diels, E. Ule 5796 (type)-F, P–663; *O. polyantha* R. E. Fries (det. L. Aristeguieta, 1967), G. T. Prance et al. 2316–NY, P–571; *O. riedeliana* R. E. Fries (det. R. E. Fries, 1937), B. A. Krukoff 5166–NY, P–572; *O. xylopioides* Diels (dupl. det. R. E. Fries), Jose M. Schunke 94–NY, P–573.

Ruizodendron *ovale* (R. & P.) R. E. Fries, G. Klug 3798–GH, P–114.

Unonopsis *buchtienii* R. E. Fries (det. R. E. Fries, 1956), Richard Evans Schultes & Isidoro Cabrera 20078–US, P–629; *U. floribunda* Diels (det. R. E. Fries, 1937), B. A. Krukoff 4806–NY, P–585; *U. glaucopetala* R. E. Fries (confirmed Fries, 1956), Bassett Maguire 40526–NY, P–586; *U. grandis* (Benth.) R. E. Fries (det. R. E. Fries, 1937), E. G. Holt & E. R. Blake 527–NY, P–587; *U. lindmanii* R. E. Fries (det. L. Aristeguieta, 1967), G. T. Prance & N. T. Silva 59526–NY, P–588; *U. mattheusii* (Benth.) R. E. Fries, G. Klug 3839–GH, P–163; *U. pacifica* R. E. Fries (det. L. Aristeguieta, 1967), J. Cuatrecasas & L. Willard 26026–US, P–631; *U. perrottettii* (A. DC.) R. E. Fries (det. R. E. Fries, 1956), Forest Dept. Brit. Guiana 6921–NY, P–589; *U. pittieri* Saff., H. Pittier 3871 (type)-US, P–628; *U. rufescens* (Baill.) R. E. Fries (det. R. E. Fries), Forest Dept. Brit. Guiana 5564–NY, P–590; *U. storkii* Standl. & L. Wms.

*Palynological accession number—cf., section on materials and methods.
†Author's collection number—cf., section on materials and methods.

(det. Louis O. Williams, 1962), V. C. Dunlap 454 (a paratype)-F, P–669; *U. veneficiorum* (Mart.) R. E. Fries (det. R. E. Fries, 1938), E. P. Killip & A. C. Smith 27086–NY, P–591.

Bocageopsis *multiflora* (Mart.) R. E. Fries (det. R. E. Fries, 1952), E. P. Killip & A. C. Smith 30077–NY, P–542.

Onychopetalum *krukoffii* R. E. Fries, B. A. Krukoff 5326 (isotype)-A, P–156; *O. lucidum* R. E. Fries, B. A. Krukoff 8214 (isotype)-A, P–157.

Monocarpia *marginalis* (Scheff.) J. Sincl., Mohd. Shah & Kadim 374–A, P–269.

Enantia *kummeriae* Engl. & Diels, P. J. Greenway 921–A, P–430.

Polyceratocarpus *parviflorus* (Bak.f.) Ghesq., J. D. Kennedy 772–US, P–621.

Desmos *cochinchinensis* Lour., Kasin (collector)—Kwai Noi River Expedition, 1946, # 161–A, P–245; *D. dumosus* (Roxb.) Saff., H. M. Burkill HMB. 1812–A, P–241; *D. dunalii* (Hk.f. & Th.) Saff., A. C. Maingay 38–GH, P–242; *D. hancei* Merr., L. Pierre 638–A, P–235; *D. insularis* A. C. Smith, Otto Degener 14968 (holotype)-A, P–243; *D. lawii* (Hk.f. & Th.) Saff., Wight 19–GH, P–236; *D. leucanthus* A. C. Smith, A. C. Smith 5613(holotype)-A, P–244; *D. monogynus* Merr., A. Petelot 2597 (isotype)-A, P–237; *D. zeylanicus* (Hk.f. & Th.) Saff., Thwaites 1037–GH, P–238.

Dasymaschalon *blumei* Finet & Gagnep., A. Denny 1120–A, P–249; *D. clusiflorum* (Merr.) Merr., P. Castro & F. Melegrito 1385–A, P–250; *D. glaucum* Merr. & Chun, S. K. Lau 27330–A, P–246; *D. macrocalyx* Finet & Gagnep., H. Y. Liang 61659–A, P–247; *D. sootepense* Craib, Th. Sorensen, Kai Larsen, & Bertel Hansen 2988–A, P–239.

Friesodielsia *bakeri* (Merr.) van Steenis, A. D. E. Elmer 15902–GH, P–502; *F. beccarii* (Diels) van Steenis, O. Beccari 3742–A, P–499; *F. glauca* (Hk.f. & Th.) van Steenis, A. C. Maingay 58–GH, P–501; *F.* ? *lagunensis* (Elmer) van Steenis, A. Loher 12079–A, P–503.

Monanthotaxis *poggei* Engl. & Diels, Jean Lebrun 2569–NY, P–567.

Enneastemon *foliosus* (Engl. & Diels) Robyns & Ghesq., G. Zenker 3001–A, P–518; *E. Mannii* (Baill.) Keay, N. W. Thomas 10603–A, P–517; *E. schweinfurthii* (Engl. & Diels) Robyns Ghesq., R. Germain 194–US, P–625 (African).

Popowia *ferruginea* (Oliv.) Engl. & Diels, Flamigni 486–A, P–493; *P. gracilis* Oliv. ex Engl. & Diels, Kirk, s.n.-GH, P–494; *P. heterantha* (H. Baill.) Diels, H. Humbert 4022–A, P–495.

Desmopsis *bibracteata* (Robinson) Saff., Walker 374; *D. brevipes* R. E. Fries, Walker 144; *D. galeottiana* (Baill.) Saff., Sesse et al. 2323–F, P–657; *D. guatemalensis* Standl. & Steyerm., Julian A. Steyermark 34304 (type)-F, P–670; *D. lanceolata* Lundell, E. Matuda 2299 (isotype)-A, P–88; *D. mexicana* R. E. Fries, Geo. B. Hinton et al. 15823–NY, P–551; *D. microcarpa* R. E. Fries, Walker 399; *D. neglecta* (A. Rich.) R. E. Fries, C. Wright 1852–GH, P–91; *D. panamensis* (Robinson) Saff., Walker 370; *D. schippii* Standl., W. A. Schipp 960 (isotype)-A, P–89; *D. stenopetala* (Donn. Smith) R. E. Fries, John Donnell Smith edid. 8496 (isotype)-GH, P–90.

Stenanona *costaricensis* R. E. Fries, R. L. Wilbur & D. E. Stone 10215–GH, P–696; S. *panamensis* Standl., G. Proctor Cooper 427 (type-sheet # 1)-F, P–672.

Reedrollinsia Walker, Walker 357.

Sapranthus *campechianus* (HBK.) Standl., H. H. Bartlett 12298–A, P–84; S. *foetidus* (Rose) Saff. ex Standl., Edward Palmer 394 (isotype)-GH, P–80; S. *ligularis* Saff. ex R. E. Fries, John Donnell Smith edid. 4508 (isotype)-GH, P–81; S. *longepedunculatus* R. E. Fries, J. N. Rose 1842–GH, P–86; S. *megistanthus* Standl. & Steyerm., Paul C. Standley 59219 (isotype)-A, P–82; S. *nicaraguensis* Seem., John Donnell Smith edid. 5041–GH, P–83; S. *palanga* R. E. Fries, Walker 407; S. sp., Walker 364; S. sp., Paul H. Allen 6202–GH, P–87.

Tetrameranthus *macrocarpus* R. E. Fries, Richard Evans Schultes & Isidoro Cabrera 17091 (isotype)-GH, P–205.

Duguetia *argentea* (R. E. Fries) R. E. Fries, R. Spruce 3814 (isotype)-GH, P–102; *D. bracteosa* Mart., Riedel (no number on sheet, but probably Riedel 493)-A, P–96; *D. caudata* R. E. Fries, B. A. Krukoff 6258 (isotype)-A, P–101; *D. dimorphopetala* R. E. Fries, Bassett Maguire et al. 41704a–GH, P–97; *D. lucida* Urb., Prestoe s.n.-GH, P–92; *D. quitarensis* Benth., A. C. Smith 2483–A, P–94; *D. rhizantha* (Eichl.) Hub A. Glaziou 18842–A, P–100; *D. stelechantha* (Diels) R. E. Fries, B. A. Krukoff 1107–A, P–95; *D. stenantha* R. E. Fries, Ducke 1796–GH, P–99; *D. uniflora* (Dun.) Mart., J. J. Wurdack & L. S. Adderley 43145–GH, P–98.

Uvaria *baillonii* Guillaumin, I. Franc (Herbier of)-Prony 1736–A, P–692; *U. bipindensis* Engl., G. Zenker 570–GH, P–693; *U. boniana* Finet & Gagnep., Tsang, Wai-Tak 16314–A, P–674; *U. branderhorstii* Burck, L. J. Brass 8681–A, P–687; *U. cordata* (Dunal) Alston, A. C. Maingay 24 (mixed sheet–2 labels)-GH, P–682; *U. hamiltonii* Hk.f. & Th., L. Pierre s.n.-A, P–673; *U. javana* Dunal, A. D. E. Elmer 20857–A, P–683; *U. klaineana* Engler & Diels, R. P. Klaine 156–A, P–695; *U. lobbiana* Hk.f. & Th., Griffith 434–GH, P–686; *U. micrantha* (DC.) Hk.f. & Th., L. J. Brass 8557–A, P–688; *U. pierrei* Finet & Gagnep., M. Godefroy 48–A, P–679; *U. purpurea* Bl., Tsang, Wai-Tak 16888–A, P–677; *U. rosenbergiana* Scheffer., L. J. Brass 8421–A, P–689; *U. rufa* Bl., Th. Sorensen et al. 7233–A, P–681; *U. semecarpifolia* Hk.f. & Th., Thwaites 244–GH, P–680; *U. sympetala* Merr., L. J. Brass 8241–A, P–690.

Anomianthus *dulcis* (Dunal) J. Sincl., L. Pierre 385–A, P–206.

Tetrapetalum *borneense* Merr., A. D. E. Elmer 21211 (isotype)-GH, P–207.

Ellipeia *cuneifolia* Hk.f. & Th., Griffith s.n. (isotype)-GH, P–208.

Cyathostemma *excelsum* (Hk.f. & Th.) J. Sincl., A. D. E. Elmer 21081–A, P–230; *C. micranthum* (A. DC.) J. Sincl., G. H. S. Wood SAN A 4632–A, P–229; *C. yunnanensis* Hu, C. W. Wang 74547 (isotype)-A, P–228.

Enicosanthum *acuminatum* (Thw.) Airy-Shaw, Thwaites C.P. 3653–GH, P–281; *E. grandifolium* (Elmer) Airy-Shaw, C. A. Wenzel 92–A, P–217; *E. paradoxum* Becc., G. H. S. Wood & J. Wyatt-Smith SAN A 4257–A, P–212.

Cleistopholis *glauca* Pierre ex Engl. & Diels, G. Troupin 6340–US, P–607; *C. patens* (Benth.) Engl. & Diels, J. Mildbraed 10640–A, P–220.

Friesodielsia *discostigma* (Diels) van Steenis, G. Zenker 516–GH, P–506 and US, P–606; *F. gracilipes* (Benth.) van Steenis, G. Zenker 360–GH, P–507 and US, P–605 (African).

Sageraea *glabra* Merr., M. Ramos 1683–GH, P–225; *S. lanceolata* Miq., G. H. S. Wood SAN 16115–A, P–223; *S. thwaitesii* Hk.f. & Th., Thwaites 2702 (isotype)–GH, P–222.

Stelechocarpus *burahol* (Bl.) Hk.f. & Th., many collections–Java, from a packet of Merrill's-A, P–226.

Alphonsea *elliptica* Hk.f. & Th., Kiah S.F.N. 32312–A, P–260; *A. hainanensis* Merr. & Chun, S. K. Lau 3323–A, P–254; *A. javanica* Scheff., Beccari 2621–A, P–261; *A. lutea* (Roxb.) Hk.f. & Th., Thwaites C.P. 3826–GH, P–289; *A. mollis* Dunn, A. Henry 11, 923 (cited as 12,923 by Dunn-isotype)-A, P–252; *A. monogyna* Merr. & Chun, F. C. How 70380–A, P–253; *A. philastreana* Pierre ex Finet & Gagnep., L. Pierre 1743–A, P–256; *A. tonquinensis* A. DC., A. Petelot 4863–A, P–257; *A. ventricosa* Hk.f. & Th., Herb. Hort. Bot. Calcuttensis s.n.–from Herb. Royal Gardens, Kew-GH, P–258; *A. zeylanica* Hk.f. & Th., Thwaites C.P. 1039–A, P–259.

Rauwenhoffia *leichhardtii* (F. Muell.) Diels, L. J. Brass 7584–A, P–266; *R. oligocarpa* Diels, C. E. Carr 11789–A, P–267; *R. siamensis* Scheff., M. Eng. Poilane 22686–A, P–265.

Polyalthia *asteriella* Ridley, Kiah S.F.N. 35043–A, P–292; *P. cauliflora* Hk.f. & Th., Kiah S.F.N. 32125–A, P–293; *P. cerasoides* (Roxb.) Benth. & Hk.f. ex Bedd., H. Y. Liang 61634–A, P–276; *P. cheliensis* Hu, C. W. Wang 75757 (isotype)-A, P–273; *P. cinnamomea* Hk.f. & Th., Kiah S.F.N. 36000–A, P–294; *P. evecta* (Pierre) Finet & Gagnep., L. Pierre 1762–A, P–283; *P. forbesii* F. Muell. ex Diels, P. van Royen 3822–A, P–308; *P. glauca* (Hassk.) Boerl., L. J. Brass 7622–A, P–309; *P. hookeriana* King, Ngadiman S.F.N. 36859–A, P–296; *P. hypoleuca* Hk.f. & Th., Ngadiman S.F.N. 36697–A, P–297; *P. insignis* (Hk.f.) Airy-Shaw, G. H. S. Wood & J. Wyatt-Smith SAN A 4325–A, P–298; *P. jenkensii* (Hk.f. & Th.) Hk.f. & Th., Griffiths s.n. (type material)-GH, P–299; *P. jucunda* (Pierre) Finet & Gagnep., L. Pierre 1795 (cited by F. & G. as Pierre 179)–A, P–285; *P. laui* Merr., S. K. Lau 1796–A, P–278; *P. nemoralis* Aug DC., F. C. How 70749–A, P–279; *P. nitidissima* Benth., L. J. Brass 8733–A, P–310; *P. oblongifolia* Burck., L. J. Brass 8136–A, P–311; *P. rumphii* (Bl.) Merr., N. K. Chun & C. L. Tso 43798–A, P–275, also A. D. E. Elmer 21196–GH, P–302; *P. tenuipes* Merr., P. W. Richards 2306–A, P–306; *P. thorelii* (Pierre) Finet & Gagnep., L. Pierre 1506–A, P–291; *P. venosa* Merr., M. Ramos & G. Edano B.S. 36558–A, P–312; *P. xanthopetala* Merr., A. D. E. Elmer 21161–GH, P–307.

Meiogyne *lucida* Elmer, C. A. Wenzel 645–GH, P–319; *M. philippinensis* Elmer, A. D. E. Elmer 11318–A, P–320; *M. virgata* (Bl.) Miq., M. R. Henderson 18360–A, P–318.

Chieniodendron *hainanense* Tsiang & P. T. Li, N. K. Chun & C. L. Tso 44583–A, P–317.

Mezzettia *havilandii* Ridley, A. Cuadra A 1304–A, P–321; *M. leptopoda* (Hk.f. & Th.) Oliv. in Hk.f., G. H. S. Wood SAN 17069–A, P–324; *M. parviflora* Becc., O. Beccari 2588–A, P–322; *M. umbellata* Becc., J. Sinclair & Kadim 10417–A, P–323.

Woodiella *sympetala* Merr., M. Ramos 1562–A, P–332.

Neouvaria *acuminatissima* (Miq.) Airy-Shaw, H. G. Gutierrez 78103–A, P–348.

Papualthia *lanceolata* (Vidal) Merr., M. Ramos B.S. 33052–A, P–328; *P. loheri* (Merr.) Merr., E. D. Merrill 10457–A, P–329; *P. reticulata* (Elm.) Merr., C. A. Wenzel 1777–GH, P–330; *P. urdanetensis* (Elm.) Merr., A. D. E. Elmer 13931 (isotype)-A, P–331; *P.* sp., L. J. Brass 1436–A, P–327.

Miliusa *balansae* Finet & Gagnep., A. Petelot 6297–A, P–334; *M. campanulata* Pierre, A. Petelot 1817–A, P–335; *M. chunii* W. T. Wang, F. C. How & N. K. Chun 70164–A, P–333; *M. indica* Leschen. ex A. DC., L. L. Uhl (Father Anglade Collection) s.n.-A, P–336; *M. velutina* Hk.f. & Th., M. Poilane 14892–A, P–338.

Saccopetalum *arboreum* Elm., A. D. E. Elmer 12677 (isotype)-A, P–343; *S. horsfieldii* Benn., Kostermans & Kuawatu 55–A, P–341; *S. longipes* Vidal, M. Ramos & D. Deroy 22573–A, P–342; *S. tomentosum* Hk.f. & Th., Joseph Fernandes 1066–A, P–340.

Fissistigma *acuminatissimum* Merr., A. Petelot 5797 (holotype)-A, P–365; *F. elmeri* Merr.. A. D. E. Elmer 20881 (isotype)-GH, P–381; *F. glaucescens* (Hance) Merr., F. C. How 73060–A, P–360; *F. latifolium* (Dunal) Merr., A. D. E. Elmer 20516–A, P–380; *F. rufum* (Presl.) Merr., A. D. E. Elmer 16709–A, P–383; *F. stenopetalum* (F. Muell.) R. E. Fries, S. T. Blake 15822–A, P–356; *F. villosissimum* Merr., A. Petelot 2683 (holotype)-A, P–370.

Mitrella *kentii* (Bl.) Miq., Griffith 389–GH, P–388.

Melodorum *aberrans* (Maingay ex Hk.f. & Th.) J. Sincl., L. Pierre 1317bis–A, P–728; *M. fruticosum* Lour., Bejeauo 598–A, P–729.

Oncodostigma *monosperma* (Hk.f. & Th.) J. Sincl., A. C. Maingay 100 (isotype)-GH, P–390; *O. wilsonii* Guillaum. J. P. Wilson 986 (isotype)-A, P–391.

Guamia *mariannae* (Saff.) Merr., S. F. Glassman 306–A, P–392.

Artabotrys *cumingiana* Vidal, M. Ramos B.S. 39810–A, P–399; *A. harmandii* Finet & Gagnep., L. Pierre 423 (syntype)-A, P–393; *A. stenopetalus* Engl., C. Vigne 1652–A, P–404; *A. suaveolens* (Bl.) Bl., Kiah S.F.N. 35970–A, P–395; *A. trichopetalus* Merr., A. D. E. Elmer 20489–A, P–396; *A. uncinatus* (Lam.) Merr., Walker 440.

Cyathocalyx *insularis* A. C. Smith, Otto Degener 14638–A, P–426; *C. martabanicus* Hk.f. & Th., Harmand 1112–A, P–417; *C. papuanus* Diels, P. van Royen 3586–A, P–423; *C. petiolatus* Diels, A. Floyd 7005–A, P–425; *C. ridleyi* (King) J. Sincl., E. J. H. Corner S.F.N. 21317–A, P–420; *C. suaveolens* A. C. Smith, A. C. Smith 9483–GH, P–427; *C. sumatranus* Scheff., M. R. Henderson S.F.N. 24533–A, P–421.

Drepananthus *apoensis* Elm., M. Ramos B.S. 24322–A, P–414; *D. carinatus* Ridley, P. W. Richards 1282–A, P–410; *D. pahangensis* Hend., Ngadiman S.F.N. 36855, P–412; *D. philippinensis* Merr., M. Ramos & G. Edano B.S. 33752–A, P–415; *D. ramuliflorus* Maing. ex Hk.f. & Th., P. W. Richards 1187–A, P–413.

Orophea *bracteolata* Merr., M. Ramos B.S. 27471–A, P–439; *O. cumingiana* Vidal, A. D. E. Elmer 16688–A, P–440; *O. ellipanthoides* (Elm.) Merr.=*Pseuduvaria* sp. (?), M. Ramos & G. Edano B.S. 36636–A, P–441; *O. enterocarpa* Maingay ex Hk.f. & Th., Kiah S.F.N. 32058–A, P–435; *O. enterocarpoidea* Vidal, Elmer D. Merrill 1815–GH, P–442; *O. leytensis* Merr., C. A. Wenzel 1723–GH, P–443; *O. luzonensis* Merr. =*Pseuduvaria* sp. (?), R. S. Williams 510–GH, P–444; *O. polyantha* Merr., M. Ramos 1673 (isotype)-GH, P–446; *O. vulcanica* Elm., A. D. E. Elmer 16312 (a syntype)-A, P–447.

Platymitra *macrocarpa* Boerl., Koorders 24576, 15679–many collections (Java), P–449.

Mitrephora *fragrans* Merr., P. Natividad F.B. 25755–A, P–481; *M. glabra* Scheff., P. W. Richards 2223–A, P–478; *M. macrantha* Hassk., Djoemadi N. 124 (Bogor Botanic Gardens XXV. A. 4)–A, P–479; *M. samarensis* Merr., M. Ramos 1666 (isotype)-GH, P–485; *M. thorelii* Pierre, C. Wang 36294–A, P–476; *M. weberi* Merr., C. M. Weber 1550–A, P–483; *M. williamsii* C. B. Rob., A. De Mesa F.B. 27464–A, P–484.

Pseuduvaria *philippinensis* Merr., M. Ramos B.S. 46374–A, P–474; *P. reticulata* (Bl.) Miq., G. H. S. Wood SAN A 2948–A, P–471; *P. rugosa* (Bl.) Merr., Th. Sorensen et al. 681–A, P–470; *P. versteegii* (Diels) Merr., L. J. Brass 7311–A, P–473.

Popowia *fusca* King, Kiah S.F.N. 31923–A, P–490; *P. odoardii* Diels, Haji Bujang 14364–A, P–488; *P. pachypetala* Diels, R. Schlechter 18873 (type material)-A (not *Annonaceae!*), P–491; *P. pisocarpa* (Bl.) Endl., A. D. E. Elmer 20735–A, P–489; *P. polytricha* Diels, L. J. Brass 586 (isotype)-A, P–492.

Phaeanthus *crassipetalus* Becc., O. Beccari 2508–A, P–508; *P. ebracteolatus* (Presl.) Merr., C. A. Wenzel 1737–A, P–511.

Trivalvaria *macrophylla* (Bl.) Miq., Kiah S.F.N. 35393–A, P–512; *T. nervosa* (Hk.f. & Th.) J. Sincl., E. J. H. Corner S.F.N. 29032–A, P–513.

Guatteria *oliviformis* Donn. Smith, Walker 413.

Guatteriopsis *sessiliflora* (Benth.) R. E. Fries (det. R. E. Fries), A. Ducke 23892–US, P–610.

Heteropetalum *brasiliense* Benth., Bassett Maguire et al. 36371–GH, P–125.

Anaxagorea *acuminata* (Dun.) St. Hil. ex A. DC., H. S. Irwin et al. 54545–NY, P–532; *A. brachycarpa* R. E. Fries (dupl. det. R. E. Fries, 1956), Bassett Maguire et al. 36789–NY, P–533; *A. brevipes* Benth. in Hk.f. (dupl. det. R. E. Fries, 1955), Bassett Maguire et al. 29792–NY, P–534; *A. costaricensis* R. E. Fries (author's preserved material–no voucher), P–184; *A. dolichocarpa* Sprague & Sandw. (confirmed Fries, 1956), Richard S. Cowan & Jon C. Linderman 39104–NY, P–535; *A. megalophylla* R. E. Fries, B. A. Krukoff 4700–F, P–652; *A. minor* Diels ex R. E. Fries (cited in Fl. Peru), E. P. Killip & A. C. Smith 28610–US, P–618; *A. multiflora* R. E. Fries, Forest Dept. Brit. Guiana 7191–NY, P–537; *A. mutica* R. E. Fries (det. R. E. Fries, 1937),

B. A. Krukoff 5057–NY, P–538; *A. phaeocarpa* Mart. (det. R. E. Fries), A. Ducke 19631–US, P–619; *A. prinoides* (Dun.) St. Hil. (det. R. E. Fries, 1956), Richard S. Cowan 38515–NY, P–539.

Piptostigma *(Brieya) fasciculatum* (De Wild.) Boutique, C. Vigne 2057–A, P–352; *P. glabrescens* Oliv., G. Mann 1792–GH, P–351 and G. Zenker 505–GH, P–350; *P. multinervium* Engl. & Diels, G. Zenker 2263 (isotype)-A, P–349.

Xylopia *aethiopica* (Dunal) A. Rich., Kersting A. 181–A, P–723; *X. africana* (Benth.) Oliv., Deistel 151–A, P–724; *X. aromatica* (Lam.) Mart., Alexander F. Skutch 4339–A, P–699; *X. brasiliensis* Spreng., E. Hassler 10714–A, P–704; *X. densiflora* R. E. Fries, G. Klug 3923 (isotype)-GH, P–712; *X. discreta* (L.f.) Sprague & Hutchinson, A. C. Smith 2596–A, P–705; *X. ferruginea* (Hk.f. & Th.) Hk.f. & Th., E. J. H. Corner S.F.N. 30382–A, P–718; *X. frutescens* Aubl., Walker 138; *X. laevigata* (Mart.) R. E. Fries, A. Glaziou 1530–A, P–709; *X. macrantha* Tr. & Pl., W. N. Bangham 490–A, P–700; *X. micans* R. E. Fries, G. Klug 3034 (isotype)-GH, P–711; *X. nitida* Dunal, Sagot 1046–GH, P–706; *X. poeppigii* R. E. Fries, G. Klug 3048–A, P–707; *X. polyantha* R. E. Fries, B. A. Krukoff 8150–A, P–708; *X. sericea* St. Hil., Riedel 2697–A, P–710.

Fusaea *decurrens* R. E. Fries, Richard Evans Schultes & Isidoro Cabrera 16039–GH, P–103; *F. longifolia* (Aubl.) Saff. (det. L. Aristeguieta, 1967), G. T. Prance et al. 4594–NY, P–560.

Duckeanthus *grandiflorus* R. E. Fries (det. R. E. Fries, 1950), J. Murca Pires 444–NY, P–554.

Cananga *latifolia* (Hk.f. & Th.) Finet & Gagnep., M. Poilane 15082–A, P–272; *C. odorata* (Lam.) Hk.f. & Th., Walker 123.

Meiocarpidium *lepidotum* (Oliv.) Engl. & Diels, F. J. Breteler 1398–A, P–271.

Neostenanthera *gabonensis* (Engl. & Diels) Exell, G. P. Cooper 416–GH, P–407; *N. hamata* (Benth.) Exell, G. P. Cooper 371–F, P–666; *N. myristicifolia* (Oliv.) Exell. Ghesquiere 2820–A, P–408.

Goniothalamus *amuyon* (Blanco) Merr., M. Ramos B.S. 32705–A, P–466; *G. chartaceus* Li, W. T. Tsang 30097 (isotype)-A, P–453; *G. curtisii* King, Nur 11191–A, P–457; *G. grandiflorus* (Warb.) Boerl., L. J. Brass 8002–A, P–465; *G. nitidus* Merr., M. Ramos 1724–A, P–459; *G. puncticulifolius* Merr., M. Ramos B.S. 39660–A, P–468; *G. repevensis* Pierre ex Finet & Gagnep., L. Pierre 607 (a syntype)-A, P–455; *G. saigonensis* Pierre ex Finet & Gagnep., L. Pierre–no number on sheet, but probably Pierre 1796 (then a syntype)-A, P–456; *G. velutinus* Airy-Shaw, J. Sinclair & Kadim 10429–A, P–462.

Richella *monosperma* A. Gray, John W. Gillespie 3652–GH, P–505.

Monodora *angolensis* Welw., Ghesquiere 2845–A, P–523; *M. brevipes* Benth., G. P. Cooper 83–A, P–524; *M. junodii* Engl. & Diels, L. E. Godd & R. A. Dyo 4539–NY, P–569; *M. myristica* (Gaertn.) Dunal, F. J. Breteler et al. 2267–A, P–526; *M. tenuifolia* Benth., G. Zenker 64–GH, P–527.

Isolona *campanulata* Engl. & Diels, M. Aubreville 570–A, P–528; *I. congolana* (De Wild. & Th. Dur.) Engl. & Diels, R. Germain 278–US, P–644; *I. hexaloba* (Pierre ex Engl. & Diels) Engl. & Diels, J. D. Kennedy 1568–A, P–530; *I. pilosa* Diels, Gossweiler 9063–US, P–646.

Uvariastrum *hexaloboides* (R. E. Fries) R. E. Fries, C. E. Duff & R. G. Miller 300/35–A, P–344; *U. pierreanum* Engl., Jas. D. Kennedy 2571–A, P–345; *U. zenkeri* Engl. & Diels, G. Zenker 481–GH, P–346.

Uvariopsis *guineensis* Keay, D. H. Linder 580–A, P–521; *U. zenkeri* Engl., G. Zenker 515–GH, P–522.

Hexalobus *monopetalus* (A. Rich.) Engl. & Diels, H. J. Schlieben 7432–NY, P–563.

Cleistochlamys *kirkii* (Benth.) Oliv., Menyharth 790–A, P–233.

Diclinanona *calycina* (Diels) R. E. Fries (det. R. E. Fries, 1933), G. Klug 96–US, P–643.

Asimina *longifolia* Kral, R. Kral 2335–GH, P–188; *A. obovata* (Willd.) Nash, L. J. Brass 14757–GH, P–189; *A. parviflora* (Michx.) Dunal, R. Kral 4219–GH, P–190; *A. pygmaea* (Bartr.) Dunal, R. Kral 2772–GH, P–191; *A. reticulata* Shuttlew. ex Chapm., R. Kral 6358–GH, P–192; *A. speciosa* Nash, R. Kral 2175–GH, P–193; *A. tetramera* Small, R. Kral 5372–GH, P–194; *A. triloba* (L.) Dunal, cultivated, Arnold Arboretum, P–3.

Deeringothamnus *pulchellus* Small, R. Kral 2129–GH, P–195; *D. rugelii* (B. L. Robins.) Small, R. Kral 2509–GH, P–196.

ANNONA L.

Sect. *Annona: A. aurantiaca* Barb. Rodr., B. A. Krukoff 2054–A, P–127; *A. foetida* Mart. aff., Herbert H. Smith 2418–GH, P–166; *A. montana* Macf. emend. R. E. Fries, E. L. Ekman H 9983–A, P–126; *A. muricata* L. (author's preserved material–no voucher), P–4.

Sect. *Ulocarpus* Saff.: *A. crassiflora* Mart., E. Hassler 5131–A, P–128; *A. purpurea* Moc. & Sesse ex Dunal, G. F. Gaumer & Sons 23295–GH, P–129.

Sect. *Campicola* R. E. Fries: *A. dioica* St. Hil., E. Hassler 12325–GH, P–130.

Sect. *Psammogenia* Saff.: *A. rigida* R. E. Fries, Richard Evans Schultes & Isidoro Cabrera 17530 (isotype)-GH, P–150.

Sect. *Phelloxylon* Saff.: *A. glabra* L., Walker 432.

Sect. *Helogenia* Saff.: *A. paludosa* Aubl., J. M. Pires 51904–GH, P–131; *A. senegalensis* Pers., R. P. Tisserant s.n.-A, P–168 and E. P. Phillips 1540–A, P–169; *A. stenophylla* Engl. & Diels, Anita G. Curtis 276a–GH, P–171; *A. tomentosa* R. E. Fries, Riedel 2648 (isotype)-A, P–167.

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Sect. *Oligantha* R. E. Fries: *A. amambayensis* Hassl., E. Hassler 10729 (isotype)-A, P–173; *A. cacans* Warm., J. Eugenio Leite 2098–A, P–142.

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Cymbopetalum *baillonii* R. E. Fries, Manuel Martinez 95–A, P–730; *C. brasiliense* (Vell.) Benth., J. A. Duke 4848–GH, P–731; *C. costaricense* (Donn. Smith) R. E. Fries, Walker 133, P–186 (author's preserved material); *C. gracile* R. E. Fries (det. R. E. Fries, 1955), Geo. B. Hinton et al. 10257–US (type cited as Hinton et al. 1027), P–637; *C. lanugipetalum* Schery, W. L. Stern et al. 394–US, P–638; *C. longipes* Benth. ex Diels (det. R. E. Fries), Erik Asplund 13243–NY, P–549; *C. odoratissimum* Barb. Rodr. (det. R. E. Fries, 1937), B. A. Krukoff 4646–NY, P–550; *C. penduliflorum* (Dun.) Baill., Walker 428; *C. stenophyllum* Donn. Smith, Geo. B. Hinton et al. 13788–GH, P–732; *C.* sp., Walker 122.

Cardiopetalum *calophyllum* Schlecht. (det. L. Aristeguieta, 1967), H. S. Irwin & T. R. Soderstrom 6964–NY, P–543.

Porcelia *macrocarpa* (Warm.) R. E. Fries (det. R. E. Fries), P. R. Reitz 5891–US, P–601; *P. magnifructum* (Schery) R. E. Fries, W. L. Stern & K. L. Chambers 43–A, P–202; *P. nitidifolia* Ruiz & Pav. (det. R. E. Fries, 1935), G. Klug 3750–US, P–602; *P. steinbachii* (Diels) R. E. Fries (det. R. E. Fries, 1937), B. A. Krukoff 5676–NY, P–577.

Trigynaea *caudata* (R. E. Fries) R. E. Fries (det. R. E. Fries, 1956), Forest Dept. British Guiana 7790–NY, P–583; *T. ecuadorensis* R. E. Fries, Erik Asplund 9059 (isotype)-NY, P–598; *T. oblongifolia* Schlecht. (det. R. E. Fries), F. C. Hoehne 7974–NY, P–584.

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